Bull. Br. Mus. nat. Hist. (Zool.) **58**(1): 1–20 Issued 25 June 1992

The morphology and phylogeny of the Cerastinae (Pulmonata: Pupilloidea)

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Synopsis. A cladistic analysis of cerastine genera has shown that they represent a monphyletic unit clearly distinct from the selected outgroup, the northern Enidae *sensu stricto*. The Cerastinae are broadly separable into two major clades, the more advanced, or at least more highly differentiated of which is characterised by a pseudosigmurethrous excretory system, as well as certain modifications to the reproductive system. A number of these character-state changes may be interpreted as reflecting a progressive trend towards a more xerophilic lifestyle in both clades, but which is more pronounced in pseudosigmurethrous genera. This has led to a high degree of homoplasy in certain characters. A new character, the caudal crest, is described for the first time and, within the orthurethra, appears to be restricted to the more primitive genera of Cerastinae.

INTRODUCTION

The cerastines were first recognised as being taxonomically distinct from northern representatives of the orthurethran land-snail family Enidae (Buliminidae) by Hugh Watson (1920) who, in a discussion of relationships within the Pupilloidea, commented 'there can be little doubt that *Pachnodus* and its allies should be placed in a separate subfamily from the Palaearctic forms, or perhaps even a distinct family'. The name Cerastinae was formalized by Wenz (1923) in his treatment of Miocene fossil *Cerastus*. Two years later Steenberg (1925), having discussed further the anatomical differences between northern and southern forms, proposed the family name Pachnodinae for the latter. Like Watson, Steenberg was equivocal as to whether the group should constitute a family or subfamily, reflecting the problems which then existed, and indeed still exist, in understanding the family-group taxonomy of the Pupilloidea.

The current concept of the Cerastinae is as a subfamily within the Enidae *sensu lato* (*eg*. Zilch, 1959; Tillier, 1989). However, Mordan (1984; 1986) has reviewed the anatomy of the two groups and argued that the differences between the northern enids and the cerastines are probably of sufficient magnitude for the latter to warrant full family status within the Pupilloidea, although formalisation of this was deferred pending a better knowledge of related orthurethran families. Furthermore, he pointed out that it was difficult to find synapomorphic characters to unite the Cerastinae and the northern Enidae as sister groups in a cladistic sense. Most recently Nordsieck (1986) has given the group family status as the Cerastuidae, which, together with the Buliminidae, form the superfamily Buliminoidea according to his classification.

The cerastines are of considerable interest from a biogeographical viewpoint, having a highly disjunct southern distribution centred on the Afro-tropical region, but extending to India and Australia, and there has been some uncertainty as to whether this represents an ancient vicariant pattern or is simply the result of more recent dispersal events (Mordan, 1984; Nordsieck, 1986). The importance of clearly defined phylogenetic hypotheses as a prerequisite to biogeographic interpretation has frequently been stressed (*eg*. Wiley, 1981; Humphries & Parenti, 1986). The present paper assesses the phylogenetic relationships between the genera and subgenera of Cerastinae using cladistic analysis; a second paper (Mordan, in press) considers the biogeographic implications of the resulting cladogram.

INCLUDED TAXA

In the most recent comprehensive treatment of the Cerastinae, Zilch (1959) listed a total of fifteen genera and subgenera to which a further two, *Amimopina* Solem, 1964 and *Altenaia* Zilch, 1972, have since been added. There is now at least partial published data on the soft anatomy of eleven of these taxa (see Table 1), and this has now been supplemented by further dissections of all of these except *Altenaia* (see Appendix for details of the dissections). As the cladistic analysis is based largely on characters of the soft anatomy, only taxa in the table are included; *Altenaia* is omitted from the analysis, however, as the specimen of *Altenaia connivens* (L. Pfeiffer) referred to in Zilch's paper cannot be traced (R. Janssen, in litt.) and there is therefore insufficient information on the genus. Following Connolly (1939), two forms

Table 1 Principal published sources of anatomical information on the Cerastinae.

Achatinelloides Nevill, 1878	Mordan, 1986
Altenaia Zilch, 1972	Zilch, 1972
Amimopina Solem, 1964	Solem, 1964
Cerastus Albers, 1860	Hesse, 1933; Verdcourt, 1967; Verdcourt, 1970; Mordan, 1986
Conulinus Martens, 1895	Verdcourt, 1966
Edouardia Gude, 1914	Connolly, 1925; Verdcourt, 1970
Euryptyxis Fischer, 1883	Bourguignat, 1882; Mordan, 1986
Pachnodus Albers, 1860	Van Mol & Coppois, 1980
Rachis Albers, 1850	Seshaiya, 1932
Rhachistia Connolly, 1925	Tillier, 1989
Zebrinops Thiele, 1931	Bourguignat, 1882; Mordan, 1986

of *Edouardia* are recognised in the analysis: representatives of the smaller species are separated as one group, whilst the large, carinate species from southern Africa form the second.

The anatomy of the remaining seven genus-level groups within the Cerastinae is unknown. Of these, *Polychordia* Connolly from south-west Arabia is monotypic and is most probably synonymous with *Cerastus* Albers (Mordan, 1986), as is *Paracerastus* Thiele according to Verdcourt (1970: 18). *Limicena* Connolly and *Pleurorhachis* Connolly are both small groups with restricted ranges in Malawi, Zimbabwe and Mozambique, which are separated on the basis of highly distinctive protoconch sculptures. *Passamaella* Pfeiffer represents an endemic radiation of some seven species on the Indian Ocean island of Socotra (Smith, 1903).

Following Verdcourt (1983), it was originally believed that the dissected specimens of *histrio* Pfeiffer and *chiradzuluensis* E.A. Smith belonged to the genus *Rhachidina* Thiele. However, examination of the radula clearly showed that both belong to *Rhachistia* Connolly, and as a result *Rhachidina* also is unrepresented in the analysis.

Mabilliella Ancey is restricted to eastern Africa, but although the shell is superficially similar to *Cerastus*, it differs markedly in detail from any known cerastine; Verdcourt (1983: 216) included the only species, *Mabiliella notabilis* (E.A. Smith), in the family Subulinidae, and this genus is here excluded from the Cerastinae.

CHOICE OF OUTGROUP

Selection of the outgroup in phylogenetic analysis is of critical importance for it determines the polarity of many of the morphoclinal character-state changes used in the analysis. In an earlier paper (Mordan, 1984) I mentioned that it had proved difficult to establish clear synapomorphic characters to unite the Cerastinae with the northern subfamilies of Enidae. Since then, three important studies have been published addressing the problem of the interrelationships of the Orthurethra. Nordsieck considered the significance of the reproductive and excretory systems (Nordsieck, 1985) and subsequently the shell (Nordsieck, 1986). He afforded the cerastines full family status under the name Cerastuidae, but whereas in the earlier paper the Enidae (Buliminidae) were treated as Pupilloidea, in the later one they were united with the Cerastuidae to form the superfamily Buliminoidea. No justification for this relationship was given however.

Tillier (1989), in a major review of the Stylommatophora, included the Cerastinae as a subfamily of Enidae. His study was based principally on the nervous, alimentary and excretory systems and has revealed an important synapomorpy for the Enidae *sensu lato*, namely the extreme compaction of the visceral chain. In both the northern enids and the cerastines the left parietal ganglion is in contact with both the visceral and pleural ganglia. Tillier found that this character state correlated with large size, which in itself could be considered a further synapomorphy of the combined group. Additional indirect support for the use of the northern enids (Enidae *sensu stricto*) as the outgroup comes from Nordsieck (1985) who postulated the plesiomorphous condition of the orthurethran reproductive system, to which the Enidae conform very closely.

The endemic New Caledonian Draparnaudinae were included in the Enidae by Tillier (1989), following Solem (1962). However, implicit in Tillier's interpretation is the derived nature of the group, which makes them unsuitable for use as the outgroup in the present analysis. This is most obviously manifested in the simplified genitalia (a feature shared with the Partulidae), generally recognised to be the apomorphic state in the Orthurethra (Pilsbry, 1927; Nordsieck, 1985). The Draparnaudinae are currently being revised (Tillier & Mordan, in prep.).

If it is accepted that the northern Enidae represent the most likely sistergroup of the Cerastinae, the problem remains of which enid subfamily to select as outgroup. Forcart (1940) recognised two subfamilies, the Eninae and the Chondrulinae, based on the presence or absence of a penial appendix respectively. Nordsieck (1985) argued that the presence of a penial appendix is plesiomorphic, and as both the cerastines and enines possess such an appendix, it is more appropriate that the outgroup is selected from the Eninae; the type genus, *Ena* Turton, has been chosen as representative. Comparative anatomical information on the Eninae is based on Hesse (1933), Forcart (1940) and Shileiko (1984), as well as on new dissections.

FOSSIL AND RECENT DISTRIBUTION

Putative Enidae have been recorded from as long ago as the Carboniferous in North America and Europe (Solem & Yochelson, 1979), although the earliest records of a Recent genus is *Napaeus* from the Eocene of Europe (Zilch, 1959).

Fossil data on the Cerastinae are much more limited, and are derived exclusively from the Miocene of East Africa. Newton (1914) described a *Cerastus* from the Burdigalian at Karunga Bay, Kenya, which he referred to as *C.* cf. *moellendorffi* Kobelt, a species currently living in Ethiopia and Somalia. More recently, Verdcourt (1963) has described two new species of cerastine from Kenya: one a *Cerastus*, probably related to the Ethiopian and Somali group of species; the second provisionally placed by Verdcourt in *Edouardia*, but which he thought might alternatively be a *Rachistia*. The age of these fossils has now been confirmed as Burdigalian (Lower Miocene) by Dr Peter Andrews (personal communication) who has stated that Potassium/Argon dating ages these deposits at 18.0 ma BP. Other published information on the Cerastinae is restricted to some undated fossil *Euryptyxis* from fluviatile/aeolian deposits from south-western Arabia described by Wenz (1943); from the context of the paper the deposits are unlikely to be older than Quaternary, and all the fossils are referable to Recent species. The tentative inclusion of *Procerastus* Wenz of the Eocene of Europe in the Cerastinae (Zilch, 1959) should be treated with some caution. I have examined the types of *Partula dautzenbergi* Cossman, 1906 and whilst they do resemble cerastines in a number of features, principally the fine spiral sculpture, closed umbilicus, and overall shell shape, it is difficult either to exclude or include them with confidence.

Unlike the fossils, the Recent Enidae and Cerastinae have an entirely Old-World distribution. The northern Enids are essentially Palaearctic in range, but extend southwards into northern Africa, Arabia, India and Indonesia. In contrast, the Cerastinae have a present-day distribution throughout most of Africa, south-west Arabia, peninsular India, Sri

Lanka and northern Australia/south-east New Guinea (Fig. 1). In addition, endemic genera are to be found on the Indian Ocean islands of Socotra and the Seychelles, with representatives of a few genera occurring on the Western Indian Ocean islands such as Madagascar, Comores, Aldabra and the Mascarines, and into the Pacific. The only areas of distributional overlap between the cerastines and the northern Enidae are in south-west Arabia and parts of India and Sri Lanka (Mordan, 1984).

The distributions of those genera excluded from the cladistic analysis have already been discussed above. Of those utilised in the analysis, *Rhachistia* has a widespread distribution in Africa south of the Sahara, and extends to Madagascar, India, Sri Lanka and numerous islands of the Indo-west Pacific. A single species, *Rachistia histrio*, appears recently to have spread to a number of Pacific Ocean islands such as the Celebes, New Caledonia and New Hebrides (Verdcourt, 1983). *Rachis* and *Edouardia* have similar continental distributions to *Rhachistia* occurring widely in Africa and India, but both have rather less extensive ranges in the Indian Ocean and are absent from the western Pacific. *Altenaia* is the only exclusively West African genus, being restricted to Angola and Namibia (Zilch, 1972).

Cerastus extends from northern Ethiopia and south-west Arabia down as far as northern Mozambique, and wetwards into the Congo. This genus also occurs in western India from Kutch in the north as far south as Malabar, but is absent from Oman (Mordan, 1986), although the type species, *Cerastus distans* (Pfeiffer), has Karah Island in the Arabian Gulf as its type locality. *Euryptyxis* and *Zebrinops* have similar distributions in Ethiopia, Somalia and south-west Arabia. In addition there are endemic radiations in the Seychelles (*Pachnodus*) and on Socotra (*Achatinelloides* and *Passamaella*). *Conulinus* is a small group of four species with a restricted range in East Africa (Verdcourt, 1966).

Amimopina has perhaps the most interesting distribution of all, occurring in northern Australia and south-eastern New Guinea. In Australia it extends right round the north of the continent from North-west Australia across to Queensland as far south as Proserpine (John Stanisic. *in litt.*). It is possible, however, that this genus is more widespread than previously thought, as the type series of *Bulimus subangulatus* Pfeiffer from Cambodia has recently been isolated (BMNH Reg. No. 1986166) and appears to be extremely close conchologically to topotypic material of *Amimopina beddomei* Brazier. The published type locality for the two syntypes of

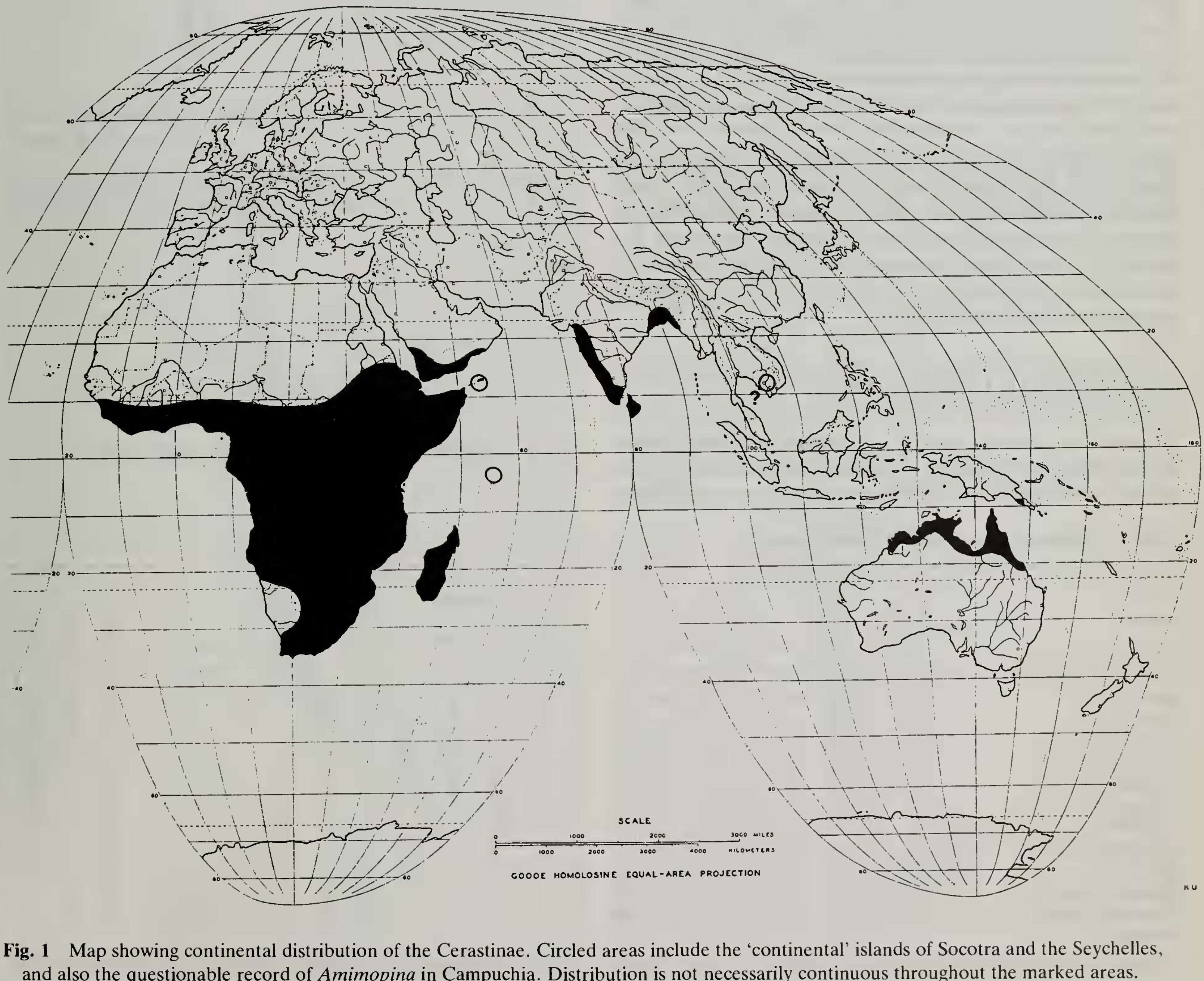

Fig. 1 Map showing continental distribution of the Cerastinae. Circled areas include the 'continental' islands of Socotra and the Seychelles, and also the questionable record of *Amimopina* in Campuchia. Distribution is not necessarily continuous throughout the marked areas.

Table 2 Character states used in phylogenetic analysis

1. Renal fold absent (0); present (1); closed (2).
2. Rectal fold absent (0); present (1); reduced (2).
3. Spermathecal stalk long (0); short (1).
4. Internal epiphallar ornamentation folds (0); Pits (1).
5. Base of central stalk of penial appendix thickened (0); not thickened (1).
6. Base of central stalk of penial appendix uncovered (0); ensheathed (1).
7. Appendicular retractor muscle inserting on basal portion of appendix (0); inserting on central stalk (1).
8. Penial and appendicular retractor muscles with joint origin (0); separate origin (1).
9. Penial retractor muscle inserting on penis (0); epiphallus (1); penis and epiphallus (2).
10. Penial caecum absent (0); elongate and well defined (1); rounded and poorly defined (2).
11. Penial pilasters/glandular pads symmetrical (0); asymmetrical (1).
12. Penial flagellum absent (0); present (1).
13. Genital atrium unpigmented (0); pigmented (1).
14. Tail crest absent (0); present (1).
15. Background shell colour dark (0); light (1).
16. Shell unpatterned (0); patterned (1).
17. Shell lip present (0); absent (1).
18. Columellar fold absent (0); present (1).
19. Umbilicus closed (0); open (1).
20. Radular row shape weakly arcuate (0); marginals angled back (1); laterals and marginals angled forwards (2).
21. Lateral teeth pointed (0); blunt (1).
22. Central tooth with ectocones (0); without (1).

subangulatus is 'Lao Mountains, Camboja' collected by Mr Mouhot. As the paper in which *Bulimus subangulatus* was originally described (Pfeiffer, 1862) included numerous other species from the same locality and collector, these data are unlikely to be in error although the possibility cannot be excluded. It must also be stressed that the soft anatomy of *subangulatus* remains unknown.

ANATOMICAL CHARACTERS

The analysis is based primarily on the anatomy of the pallial and reproductive systems, but also includes several shell and radular characters. The cerastine excretory system exhibits a

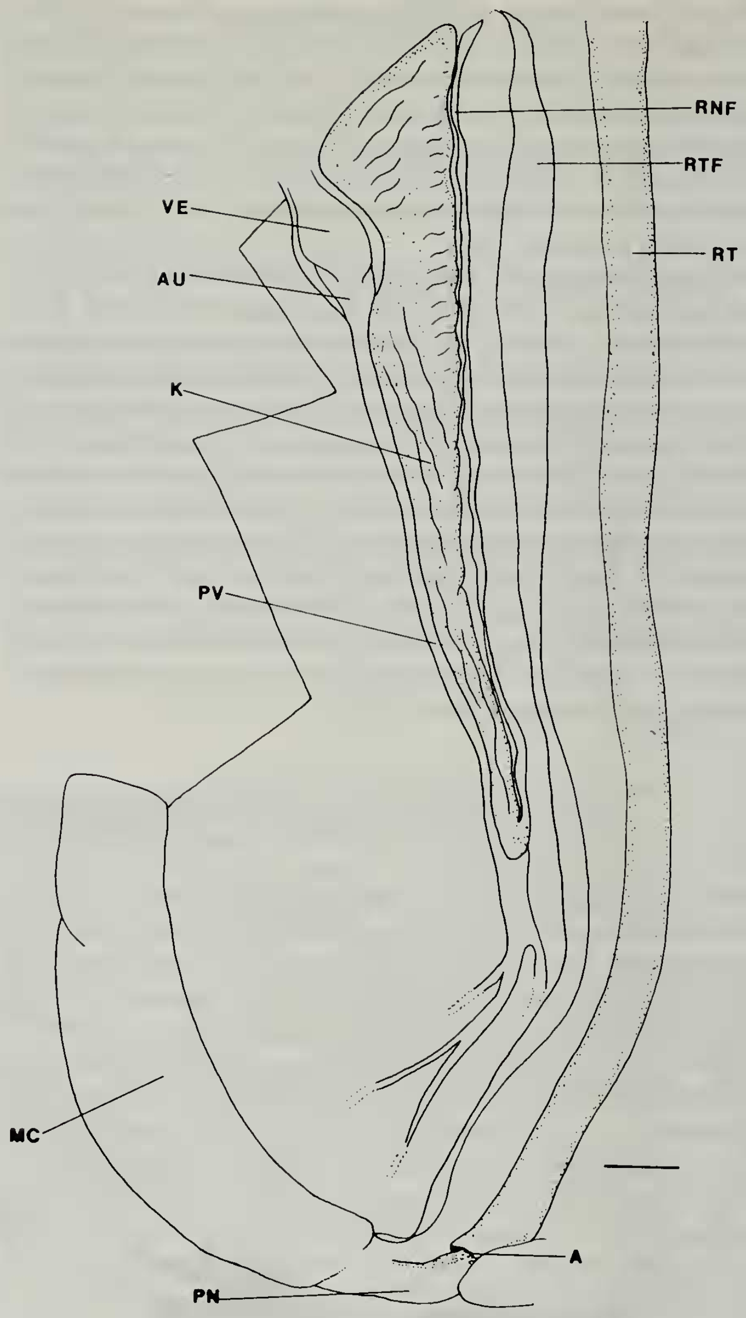

Fig. 2 *Cerastus trapezoidea*, Kitale, Kenya. Scale line 2 mm.

Table 3 Character state matrix of cerastine genera.

Genus	Character																				
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22
Ena	0	0	0	0	0	0	0	9	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Rachis	1	1	0	1	1	1	0	0	1	1	0	0	1	0	1	1	1	0	1	0	0	0
Conulinus	1	1	0	1	0	1	0	0	1	1	0	0	1	1	0	0	1	0	1	0	0	0
Zebrinops	1	1	0	1	1	1	1	1	1	1	0	0	1	0	1	1	1	0	1	0	0	0
Cerastus	1	1	0	1	0	1	1	0	1	1	0	0	9	1	0	0	0	0	1	0	0	0
Pachnodus	1	1	0	1	0	0	0	0	1	0	0	0	1	1	0	9	0	0	1	1	1	1
Euryptyxis	1	1	0	1	9	0	0	1	1	1	0	0	1	0	1	0	0	1	0	0	0	0
Achatinelloides	1	1	0	1	1	0	0	1	1	1	0	0	1	0	1	1	1	1	0	0	0	0
Rhachistia	2	9	1	0	0	0	0	9	0	2	1	1	1	0	1	1	1	0	1	2	1	1
Edouardia (small)	2	0	1	0	0	1	0	0	2	2	1	1	1	0	0	0	1	0	1	0	0	1
Edouardia (large)	2	2	1	0	0	1	0	0	2	2	1	1	1	0	0	9	1	0	1	0	0	1
Amimopina	2	1	1	0	0	0	0	0	2	2	1	1	1	0	0	0	1	0	1	2	1	1

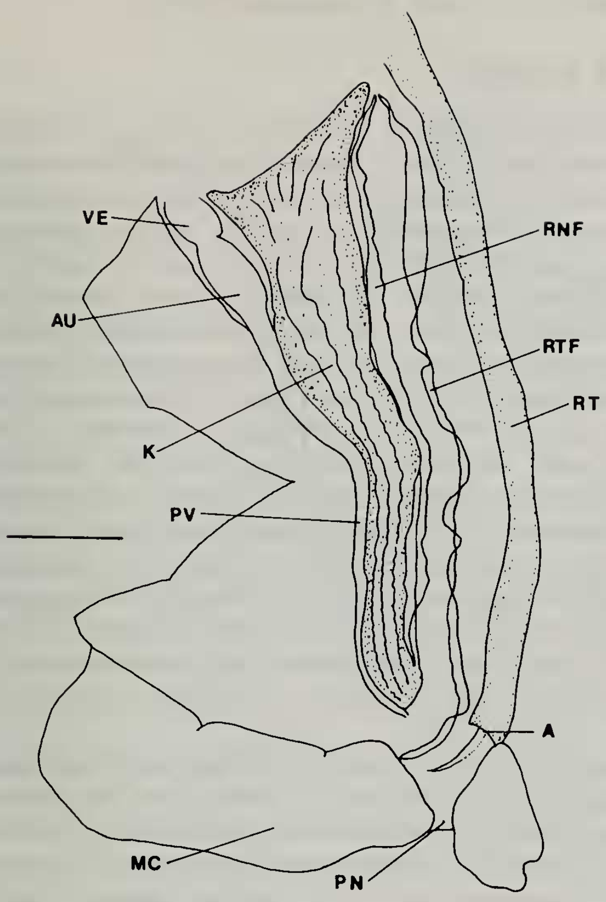

Fig. 3 Pallial complex, *Conulinus rutshuruensis*, Thika, Kenya. Scale line 2 mm.

number of new structures which themselves show a range of variation within the group, whilst the genital systems of the Arabian cerastines studied by Mordan (1986) were found to provide many useful taxonomic characters at the generic level. One external character, termed the tail crest, is also utilised as it is clearly restricted to certain genera. Table 1 lists the principal published sources of information on the anatomy of cerastines.

In choosing the characters to be used in the phylogenetic analysis (Table 2), two further factors were borne in mind: all characters autapomorphic at the generic level were excluded as these cannot contribute to the structure of the tree; secondly, it was decided not to include fully correlated characters where these appeared to be functionally related to an already coded character, as this would tend artifically to increase the consistency index of the tree (Reid, 1989).

Pallial Complex (Characters 1–2)

The excretory system of the Cerastinae exhibits a greater degree of elaboration than any other orthurethran group. In many orthurethrans, including the Enidae, a weakly developed ridge is found extending from the renal orifice along the side of the kidney to form a backwardly directed 'gutter', but in all cerastine genera a complete renal fold is developed, running the entire length of the kidney to the top of the lung cavity (Character 1). With the exception of certain small *Edouardia*, an additional fold runs downwards from a point of junction with the renal fold at the top of the lung, along the rectum as far as the pneumostome; this is termed the rectal fold (Character 2) and is not known from any other Orthurethra. In the region of the pneumostome the fold flexes away from the base of the rectum and tapers to a ridge, finally fusing with the inner wall of the mantle collar (van Mol & Coppois, 1980, Fig. 2; Mordan, 1986, Fig. 29b). A similarly

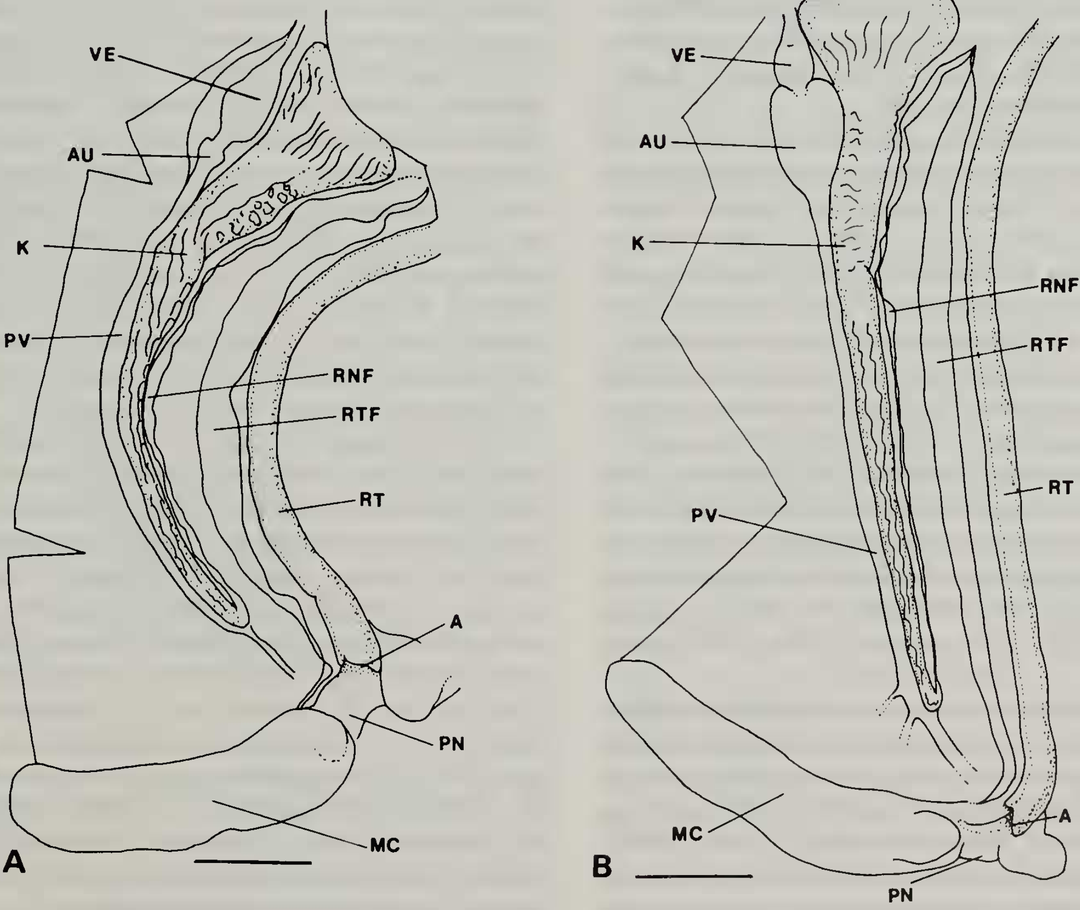

Fig. 4 Pallial complex. A. *Rachis punctata*, Dar es Salaam, Tanzania; B. *Achatinelloides socotrensis*, Socotra. Scale lines 2 mm.

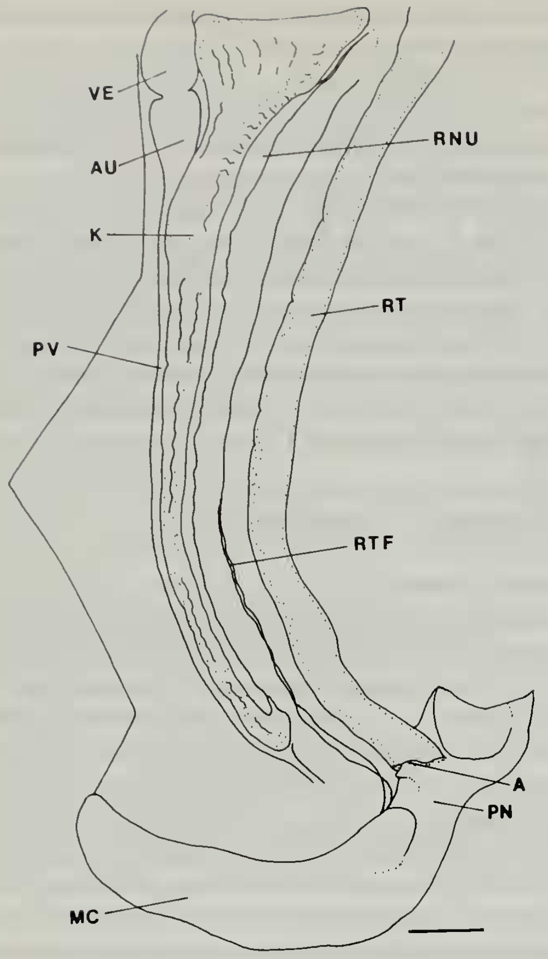

Fig. 5 Pallial complex, *Rhachistia rhodotaenia*, Nairobi-Mombassa Road, Kenya. Scale line 2 mm.

positioned and shaped pneumostomal ridge is also found in many other orthurethran families (Tillier, 1989). This arrangement of renal and rectal folds is already known from such cerastine genera as *Euryptyxis, Zebrinops* (Mordan, 1986) and *Pachnodus* (van Mol & Coppois, 1980), but is here figured also in *Cerastus* (Fig. 2), *Conulinus* (Fig. 3), *Rachis* (Fig. 4A) and *Achatinelloides* (Fig. 4B).

In a number of cerastine genera, the renal fold is fused to the kidney to form a tube—a feature first described in *Amimopina* by Solem (1964: Fig. 1) who termed it the 'pseudosigmurethrous' condition. A similar arrangement is found in *Rhachistia* (Figs 5, 6; Tillier, 1989: Fig. 137), and has also been confirmed in *Edouardia* (Fig. 7). Normally this is fused along almost its entire length to form a closed ureter, but in *Edouardia natalensis* fusion only extended about half way up the length of the kidney (Fig. 8). The presence of the pseudosigmurethrous condition is considered to be apomorphic to the possession of an unfused fold following the arguments of Tillier (1989), and consequently character 1 is ordered for the purposes of the analysis. In some species of *Rhachistia* the upper part of the rectal fold is reduced (Figs 5, 6B), although a thin ridge of tissue remains visible, and in *Edouardia* cf. *metula* (Fig. 7) it appears to be entirely missing.

Two further characteristics of the cerastine pallial complex should be noted, but were not utilised in the analysis. The prominent pallial venation, which is present in all genera, is correlated with the development of pallial folds and is thought to be a result of lung shortening (Tillier, 1989). Secondly, a well-developed mantle gland, characteristic of the northern Enidae (Mordan, 1984), was not found in any of the cerastines examined.

Reproductive System (Characters 3–13)

Penis and Epiphallus

The enine penial complex appears to be fairly uniform in structure and that of *Ena* is typical. The epiphallus enters the penis apically and the two regions are not always distinguishable externally, excepting that the top of the penis may become expanded where it contains a penial papilla. No penial caecum is present, although a structure termed the caecum does occur on the epiphallus, as does a short terminal flagellum; both are concerned with the shaping of the spermatophore (Schikow, 1978), and should not be confused with the homonymous (but not homologous) structures on the cerastine penis. Internally, both the penis and epiphallus have predominantly longitudinal pilasters. All enines possess a penial appendix of the typical orthurethran type. The basal portion of the appendix opens laterally onto the lower part of the penial tube, and also receives the insertion of the appendicular retractor muscle. The penial retractor inserts onto the top of the penis. These two muscles originate separately on the lung wall in *Ena*, but they are joined in many other enines.

The penis of the Cerastinae differs from that of the Eninae in a number of significant respects, perhaps the most obvious being the presence of a well-developed caecum in all but one genus. Two principal cerastine penial types occur. The more restricted of the two, referred to as the flagellate type, is known in *Amimopina* (Fig. 9; Solem, 1964: Fig. 2), *Edouardia* (Figs 10, 11; Verdcourt, 1967, Fig. 25), and *Altenaia* (Zilch, 1972: Fig. 5), and is also figured here from *Rhachistia* (Figs 12, 13). The penial flagellum (Character 12) is an elongate, blind-ended sac inserting on the head of the penis close to the point of entry of the epiphallus. The penial flagellum varies greatly in length; it may be as short as the penis itself or, as in *Rhachistia* and some *Edouardia*, about as long as the penial appendix. A penial caecum (Character 10) is developed in these genera but shows little differentiation internally from the rest of the penis. There are weak longitudinal pilasters in the main stem of the penis, but within the expanded apical region is a transverse glandular patch (Character 11) which is fairly extensive in *Rhachistia rhodotaenia* and *Edouardia* (Figs 14A, 15A, 16C), rather weaker in *Amimopina* (Fig. 17A) and reduced to a simple, tapering ridge in *Rhachistia histrio* (Fig. 18A). The penial retractor muscle inserts on the penis and insertion is often multiple; in *Edouardia* and *Amimopina* (Figs 15A, 17C) a lateral branch to the epiphallus was noted (Character 9).

All the remaining cerastine taxa considered here lack a penial flagellum. With the single exception of *Pachnodus*, the penis possesses a well-developed, often pointed caecum (*eg. Rachis* and *Achatinelloides*, Fig. 21), and epiphallar insertion onto the penis is more clearly lateral. Longitudinal penial pilasters are also normally better developed in this group than in flagellate forms, and usually expand apically into large, symmetrically paired, glandular patches within the caecum. The limit of the caecal area is normally distinguishable internally by a change in ornamentation (eg. *Cerastus*, Fig. 19B) or the presence of a circular ridge (*Conulinus*, Fig. 20C). As mentioned above, *Pachnodus* has no caecum, the epiphallus being continuous with the top of the penis, with no visible external demarcation between the two regions (Fig. 22A; van Mol & Coppois, 1980).

In all Cerastinae a sheath of muscle encircles the stem of

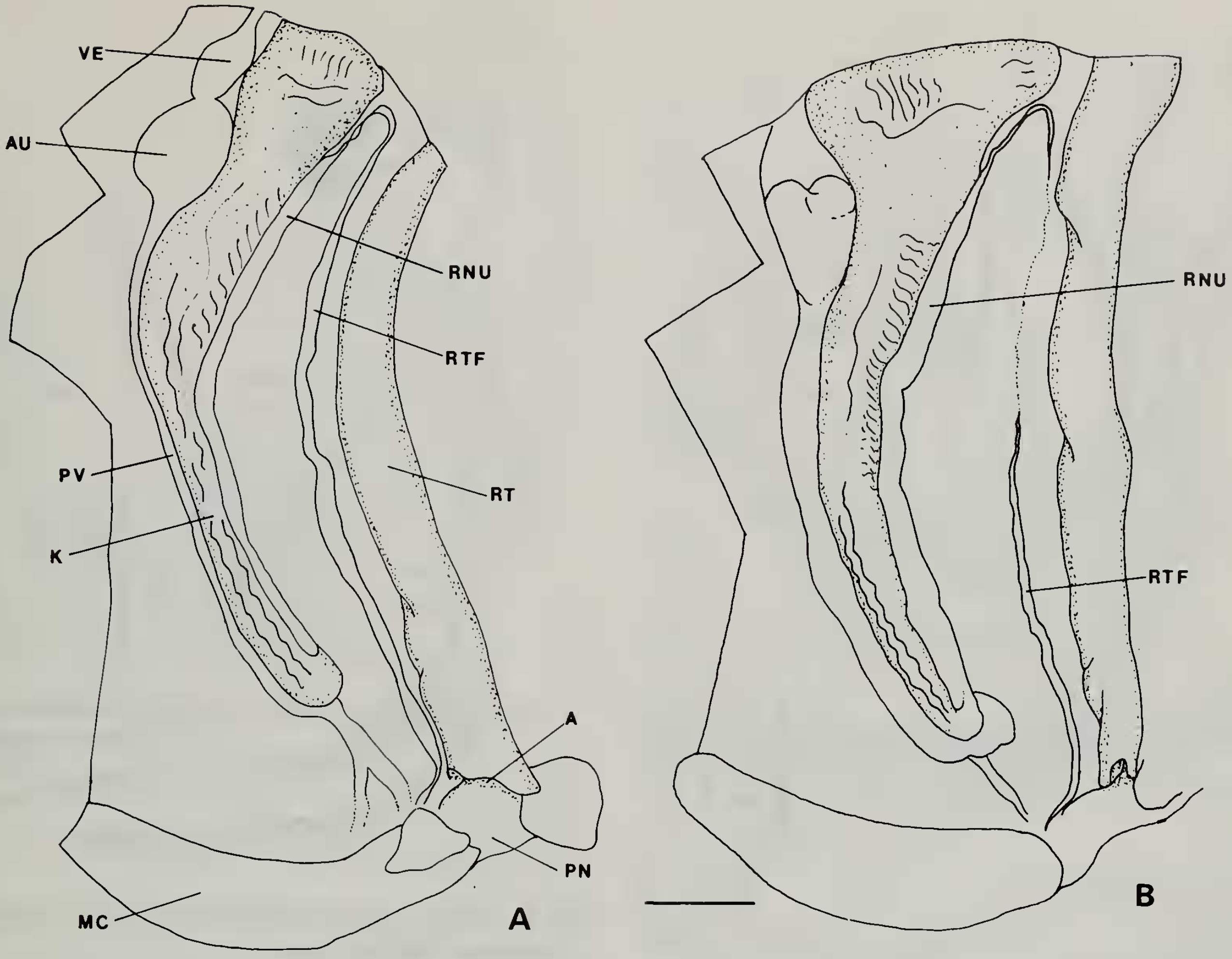

Fig. 6 Pallial complex; A. *Rhachistia chiradzuluensis*, Thika, Kenya; B. *Rhachistia histrio*, Maré, Loyalty Islands. Scale line 2 mm.

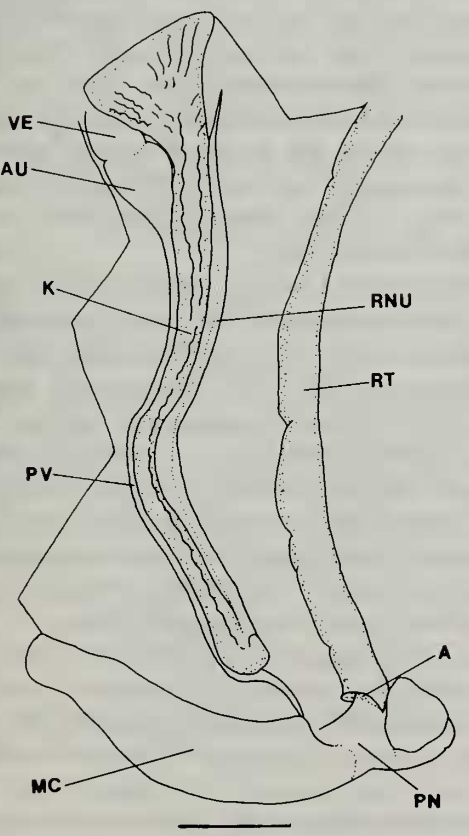

Fig. 7 Pallial complex, *Edouardia* cf. *metula*, Nairobi, Kenya. Scale line 2 mm.

the penis above the level of appendicular insertion. This is only attached at one end but may be directed upwards (eg. *Rachis*, Fig. 23A; *Pachnodus*, van Mol & Coppois, 1980, Fig. 5) or downwards (eg. *Rhachistia*, Fig. 18A; *Conulinus*, Fig. 20C) from the point of attachment. In some cases the downwardly directed muscle is recurved to form a double-layered structure (eg. *Cerastus*, Fig. 19B; *Achatinelloides*, Fig. 24A). The arrangement appears to be constant within species but, on the evidence of *Euryptyxis*, may vary between congeneric species (Mordan, 1986). The sheath is generally weaker in flagellate genera, and in *Edouardia* (Fig. 15A) is barely visible, being extremely fine, single-layered, and closely adpressed to the wall of the penis. As the sheath was found in all cerastine taxa, it was not utilised in the analysis.

The form of the cerastine epiphallus (character 4), and hence of the spermatophore which it secretes, is broadly correlated with penis type. Flagellate groups such as *Edouardia* (Figs 10, 11) and *Rhachistia* (Figs 12, 13), have an externally simple epiphallar region, only distinguishable from the vas deferens by the greater thickness of the former. Internally, the epiphallus is ornamented with longitudinal, sometimes spiral folds which in the case of *Rhachistia rhodotaenia* appear to correspond to the pair of fins which extend along about half the length of the spermatophore (Figs 14B, 25). In this species the fin becomes finely serrated along part of its length, as in some Eninae (Schikow, 1978). In contrast, the non-flagellate taxa have a spermatophore characterised by a longitudinal row of strong, discrete, hooked spines which may bear forked or complex digitiform terminations (Hesse, 1933, Fig. 43e; Mordan, 1986, Fig. 24c). The elaborate structure required to mould these spines is visible externally as a series of transverse ridges on the epiphallus (Figs 20B, 22A, 23D, 24A) and internally as a row of pits (Figs 19A, 20A,

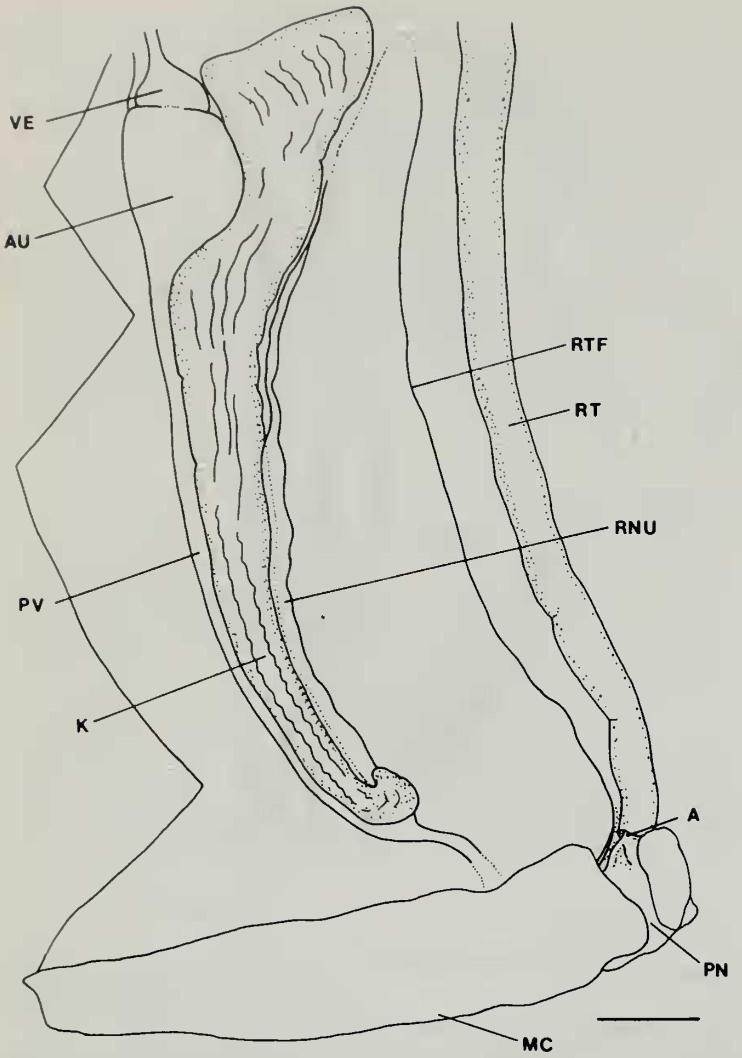

Fig. 8 Pallial complex, *Edouardia natalensis*, Pietermaritzberg, South Africa. Scale line 2 mm.

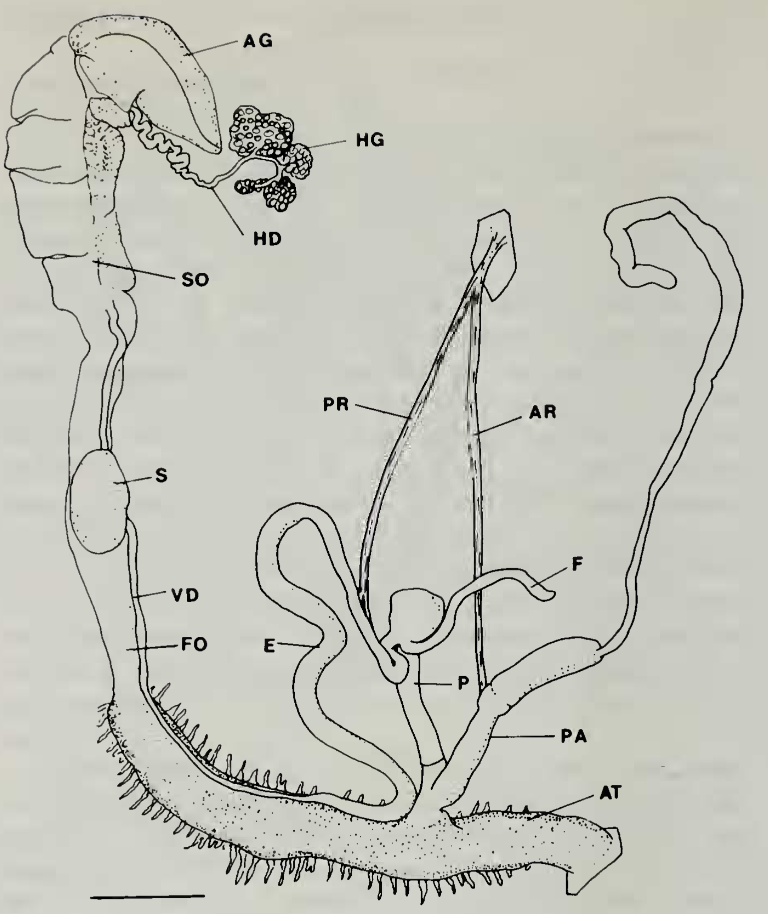

Fig. 9 Genital system. *Amimopina macleayi*, Daly River, Australia. Scale line 2 mm.

22C, 23B, 24B) which correspond in number precisely to the number of spines on the spermatophore (Mordan, 1986). In those non-flagellate taxa where even quite major modifications in spermatophore structure have taken place, such as species of *Pachnodus sensu stricto*, vestigial hooks remain (van Mol & Coppois, 1980: Figs 11; 12)

Penial appendix

A penial appendix of the typical orthurethran pattern occurs in all cerastines which have been dissected. Three principal regions of this appendix may be recognised: a wide, eversible, basal portion proximal to the penis, onto which it inserts laterally below the penial muscle sheath close to the atrium; a much narrower, thick-walled, central stalk; and an elongate terminal bulb. Shileiko (1979) has distinguished five regions by including areas of differentiation at the junction of the basal region with the central stalk (Characters 5–7), and certainly it is this particular area of the appendix which shows perhaps the greatest variation between genera, and is therefore of much taxonomic interest. Three basic structural patterns occur in this region within the Cerastinae, and these are diagramatically represented in Fig. 26.

The simplest type (Fig. 26C) is that found in *Achatinelloides* (Fig. 24C), most *Euryptyxis* (Mordan, 1986), and apparently also in some *Pachnodus* (van Mol & Coppois, 1980: Figs 5, 6), where there is a straight insertion of an undifferentiated central stalk onto the base. There may be a slight papilla at the point of entry of the stalk and a weak ring pilaster around the top of the basal lumen, and in some species belonging to the last two genera the base of the stalk may be somewhat thickened (Mordan, 1986, Fig. 23). In all three genera the appendicular retractor muscle inserts at, or just below the top of the basal portion of the appendix, although in *Euryptyxis* the muscle embraces but does not enclose the base of the central stalk prior to insertion (Mordan, 1986: Figs 30, 31b).

The second appendix type (Fig. 26D), already noted above as occurring in one species of *Euryptyxis* and some *Pachnodus* (Fig. 22B), is characteristic of *Rhachistia* (Figs 14C, 18A, D) and *Amimopina* (Fig. 17A) and possibly also *Altenaia* (Zilch, 1972: Fig. 5). Here the muscular wall of the central stalk becomes heavily thickened at its base (Character 5), the retractor again inserting at or below the top of the basal region. This is the condition found in the Eninae, and is also widespread in the Orthurethra, and is therefore considered to be the primitive state. As before, a weak papilla may protrude into the lumen of the appendix base.

In the remaining genera a thin muscular sheath actually encloses the base of the stalk (Character 6; Fig. 26A, B). Within this category there are differences in the position of the retractor muscle insertion (Character 7): *Cerastus* (Fig. 19C), and less obviously *Zebrinops* (Mordan, 1986: Fig. 37D), have the appendicular retractor inserting onto the top of the sheath (Fig. 26A), but in *Rachis* (Fig. 23C), *Conulinus* (Fig. 20D, E), and *Edouardia* (Figs 15C, 16B, C) the retractor muscle is situated in the more-usual position at or below the top of the basal region (Fig. 26B). The enclosed region of the central stalk may become elaborated internally (Figs 15C; 19C; 20D, E), and may project into the lumen of

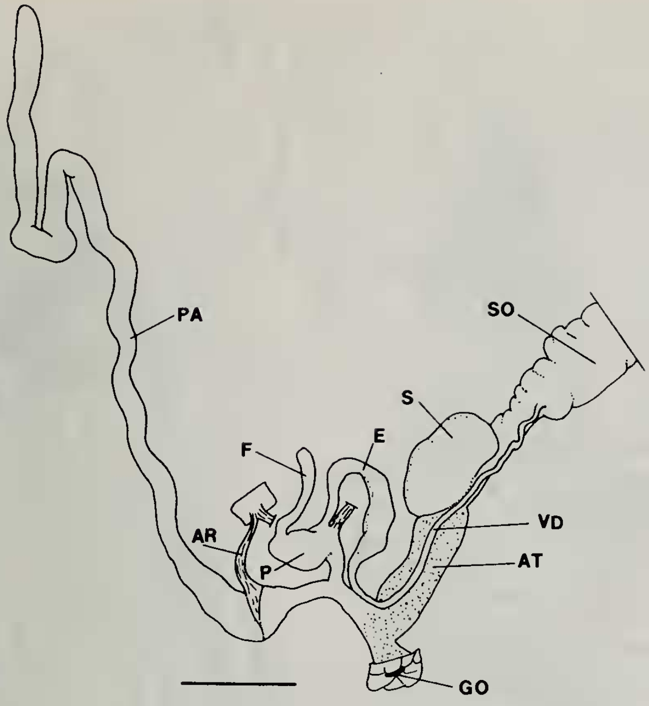

Fig. 10 Genital system. *Edouardia tumida*, Mombassa Island, Kenya. Scale line 2 mm.

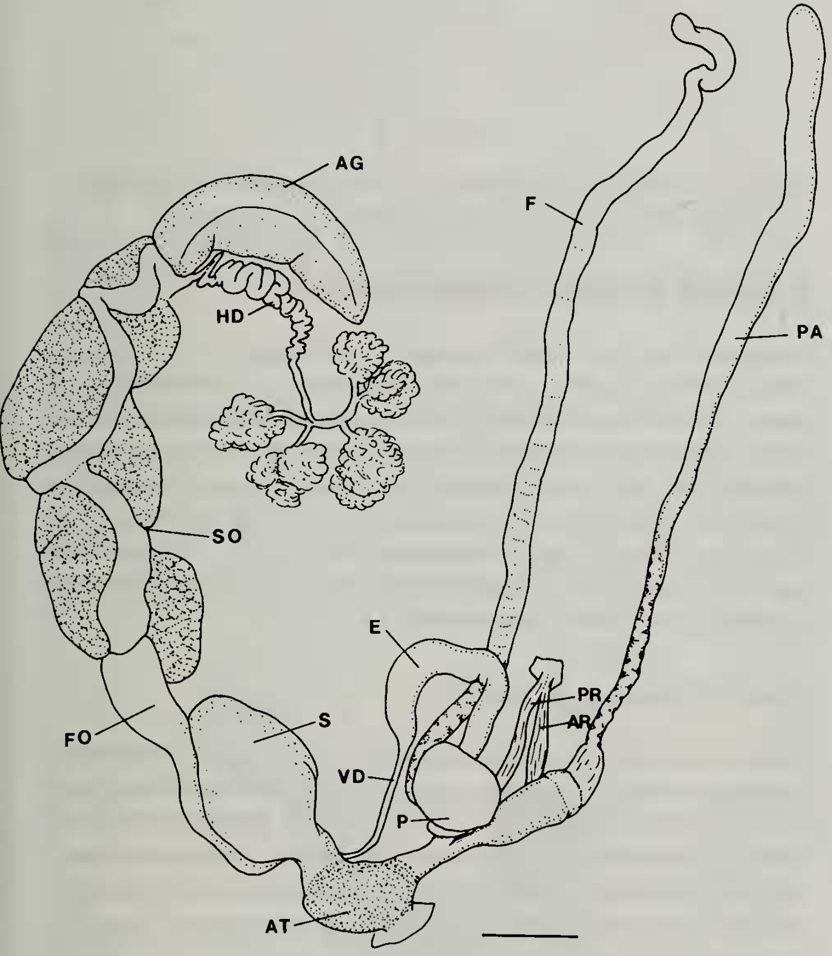

Fig. 11 Genital system. *Edouardia natalensis*, Pietermaritzberg, South Africa. Scale line 2 mm.

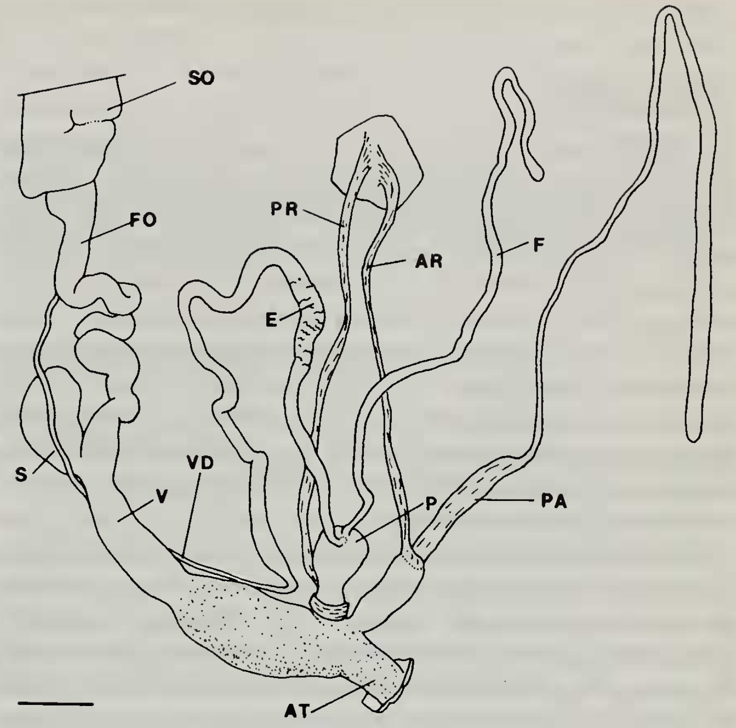

Fig. 12 Genital system. *Rhachistia rhodotaenia*, Nairobi-Mombassa Road, Kenya. Scale line 2 mm.

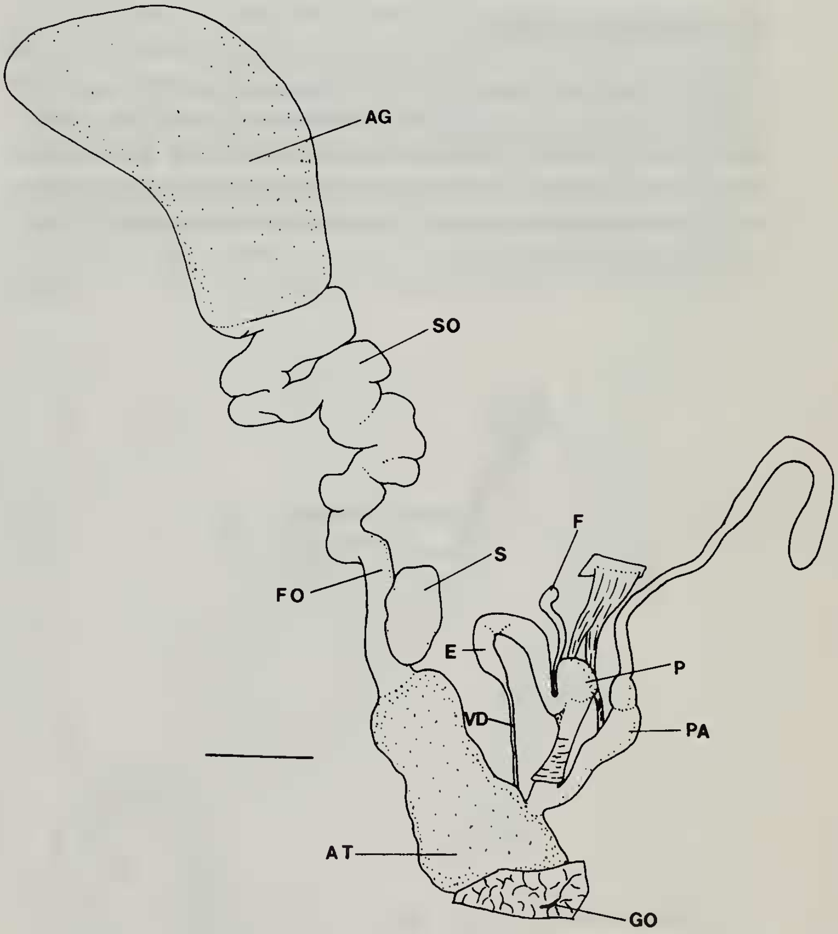

Fig. 13 Genital system. *Rhachidina histrio*, Maré, Loyalty Islands. Scale line 2 mm.

the base as a prominent papilla (*eg*. Fig. 20D). Throughout the group there is considerable variation in the extent of papillar development within species. However, this would appear to be related in large part to the degree of relaxation of the preserved specimen and thus of limited taxonomic value.

Both the appendicular and penial retractor muscles (Character 8) originate on the lower lung wall (diaphragm). In most genera (eg. *Amimopina*, Fig. 9; *Rachis*, Fig. 21A) they are joined from their origin over a considerable part of their length, whilst in others they are entirely separate (eg. *Achatinelloides*, Fig. 21B). In most enines, including *Ena*, the muscles are separate but in some they are joined. This character is thus scored as being variable for the Eninae.

Female system

The female part of the reproductive system generally shows far less variation between genera than does the male, but two features are of particular significance in respect of the Cerastinae. A highly characteristic brown spongy tissue lines the atrium and part of the vagina (Seshaya, 1932; Solem, 1964), and apparently is unique to the group (Character 13). It was present in all cerastines examined excepting *Cerastus trapezoidea* from east Africa. Its absence from certain African *Cerastus* of the *bambuseti* group to which *C. trapezoidea* belongs, has already been noted by Verdcourt (1967; 70). Histological details of this tissue in *Pachnodus* are given by van Mol & Coppois, 1980.

A second feature of interest is the form of the spermatheca (Character 3). This falls into two categories which correlate with penis structure. In genera with a flagellate penis the spermatheca lacks an obvious stalk (*Edouardia*, Figs 10, 11; *Rhachistia*, Figs 12, 13; *Amimopina*, Fig. 9; *Altenaia*, Zilch, 1972: Fig. 5), whilst in the remaining genera a clearly defined stalk or peduncle is present (*eg*. Fig. 21A, B). A spermathecal diverticulum, such as is found in many northern enid genera, has not been recorded in any Cerastinae.

Hermaphrodite system

Northern Enidae *sensu stricto* are characterised by the presence of hermaphrodite duct diverticulae (Mordan, 1984; 1986), but careful examination has not revealed these structures in any cerastine. In all cases the talon was a simple fold in the hermaphrodite duct, as recorded by Mordan (1986: Fig. 36A) for *Zebrinops*.

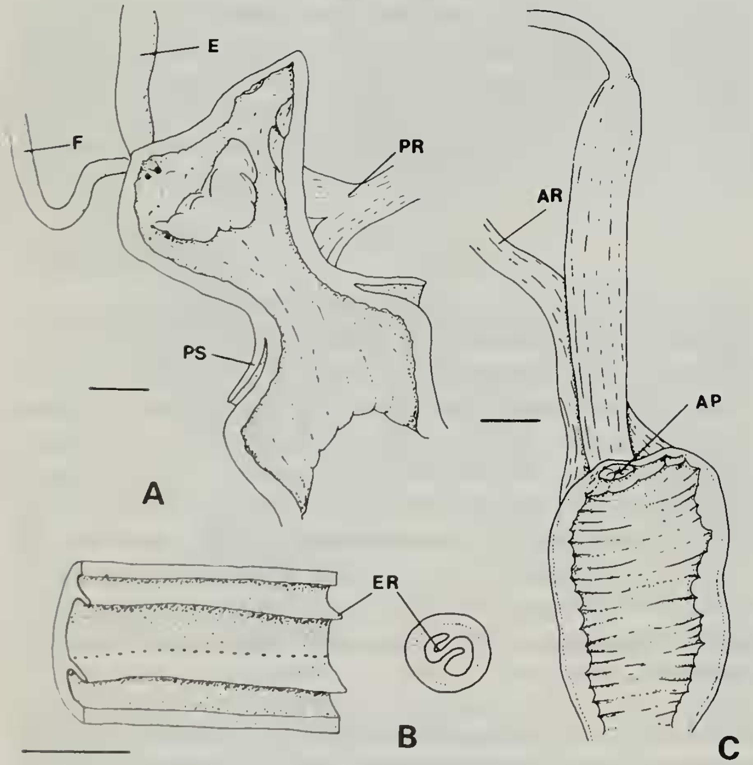

Fig. 14 A. Penis; B. Epiphallus; C. Penial appendix. *Rhachistia rhodotaenia*, Nairobi-Mombassa Road, Kenya. Scale lines 0.5 mm.

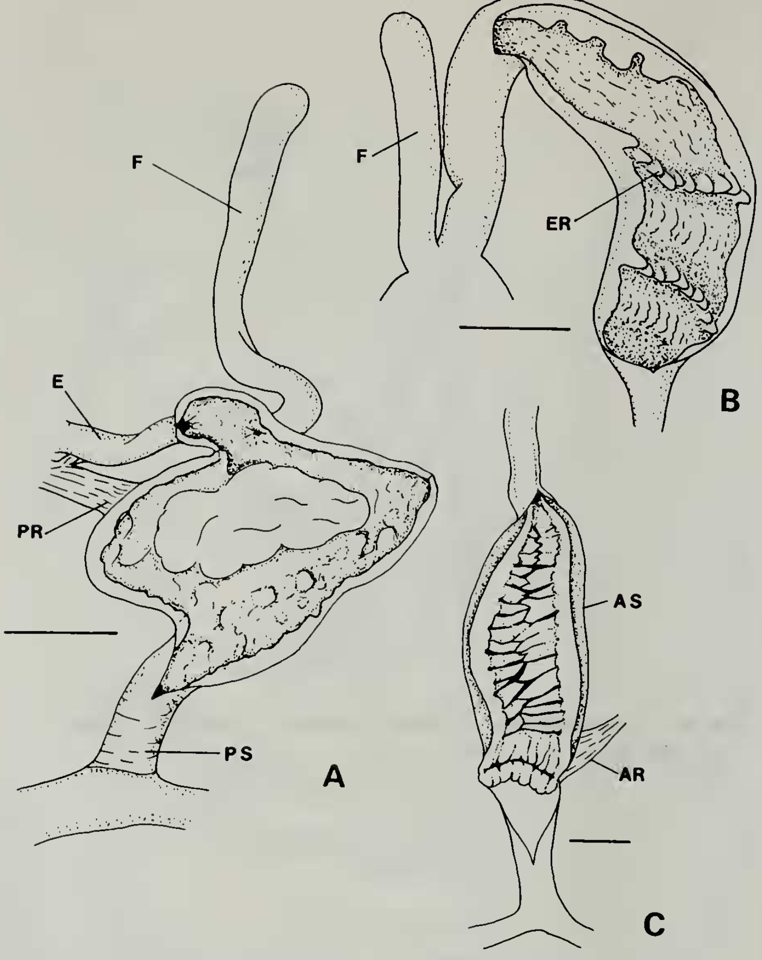

Fig. 15 A. Penis; B. Epiphallus; C. Penial appendix. *Edouardia tumida*, Mombassa Island, Kenya. Scale lines 0.5 mm.

External Features (Character 14)

Only one external body character was found to vary consistently between genera: the development of a prominent tail crest. This is situated along the dorsal mid-line of the tail and comprises a row of pointed tubercles, which are often paler in colour than the rest of the tail. The crest is clearly evident in *Cerastus, Conulinus* and *Pachnodus* (Fig. 27B–D) but not in other cerastines (eg. *Edouardia*, Fig. 27A). It does not appear to have been noted previously in the Cerastinae, nor indeed in any other orthurethran.

Shell (Characters 15–19)

Whilst most shell characteristics are, in general, remarkably consistent within cerastine genera, both size and shape are too variable to be of value in the analysis. Background shell colour (Character 15) tends either to be pale cream or brown, depending to some extent upon the thickness of the periostracal and calcareous layers. Similarly, entire genera have the propensity to develop patterning (Character 16), whereas others never do. This patterning typically takes the form of up to five spiral bands which may become broken up and fused to form a variety of characteristic patterns. These are particularly pronounced in *Rachis, Rhachistia* and *Rhachidina*, which have long been confused taxonomically, as well as in *Achatinelloides* and *Zebrinops*. Some species of *Pachnodus* and *Edouardia* develop a single, peripheral band but in both genera, species with an unpatterned shell are by far the more usual.

A lip (Character 17) only develops on the adult shell, and

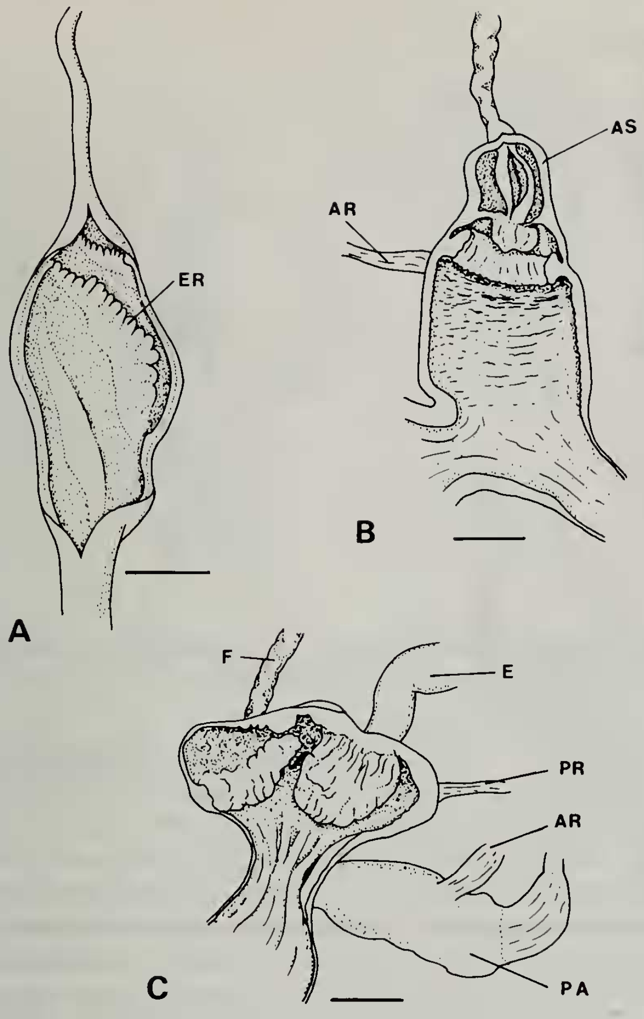

Fig. 16 A. Epiphallus; B. Penial appendix; C. Penis. *Edouardianatalensis*, Pietermaritsberg, South Africa. Scale line 1 mm.

genera were readily classified as lip present or absent. In most genera the umbilicus (Character 19) remains open, although it can vary from widely gaping (eg. *Conulinus*) to minute (eg.*Rhachistia*), but in *Euryptyxis* and *Achatinelloides* it becomes closed off. These last two genera additionally develop a columellar fold or ridge (Character 18) which is clearly visible in the aperture, and which may become considerably enlarged further back within the body whorl (Mordan, 1986).

Radula (Characters 20–22)

In separating the Cerastinae (or Pachnodinae) from the northern Enidae, Watson (1920: 23) noted that in many cerastine species 'most of the teeth of the radula, instead of having their major axes practically in a line with one another, are placed more or less obliquely, so that the outer side of one tooth is in front of the inner tooth next beyond'. In *Pachnodus* (van Mol & Coppois, 1980) there is a clear backward angulation of the marginal teeth relative to the laterals, which lie in a relatively straight row. By way of contrast, in all eleven species of *Rhachistia* and one of *Amimopina* whose radulae were examined in the present study, the entire row is angled forward in a V shape from the central tooth at a fairly constant angle of about 110°. Both these patterns are distinct from the weakly arcuate row form characteristic of the remaining cerastine genera and the Eninae (Mordan, 1986: Fig. 19e). Thus three states of radular row pattern are recognised in the analysis (Character 20). In most of the cerastines examined, tooth form is fairly uniform: the central mesocone is pointed and bears a pair of smaller ectocones; laterals have a similarly pointed mesocone with well-developed ectocone but no endocone; and the marginals carry blunt, rounded mesocones and ectocones broken up into a series of pointed cusps which becom

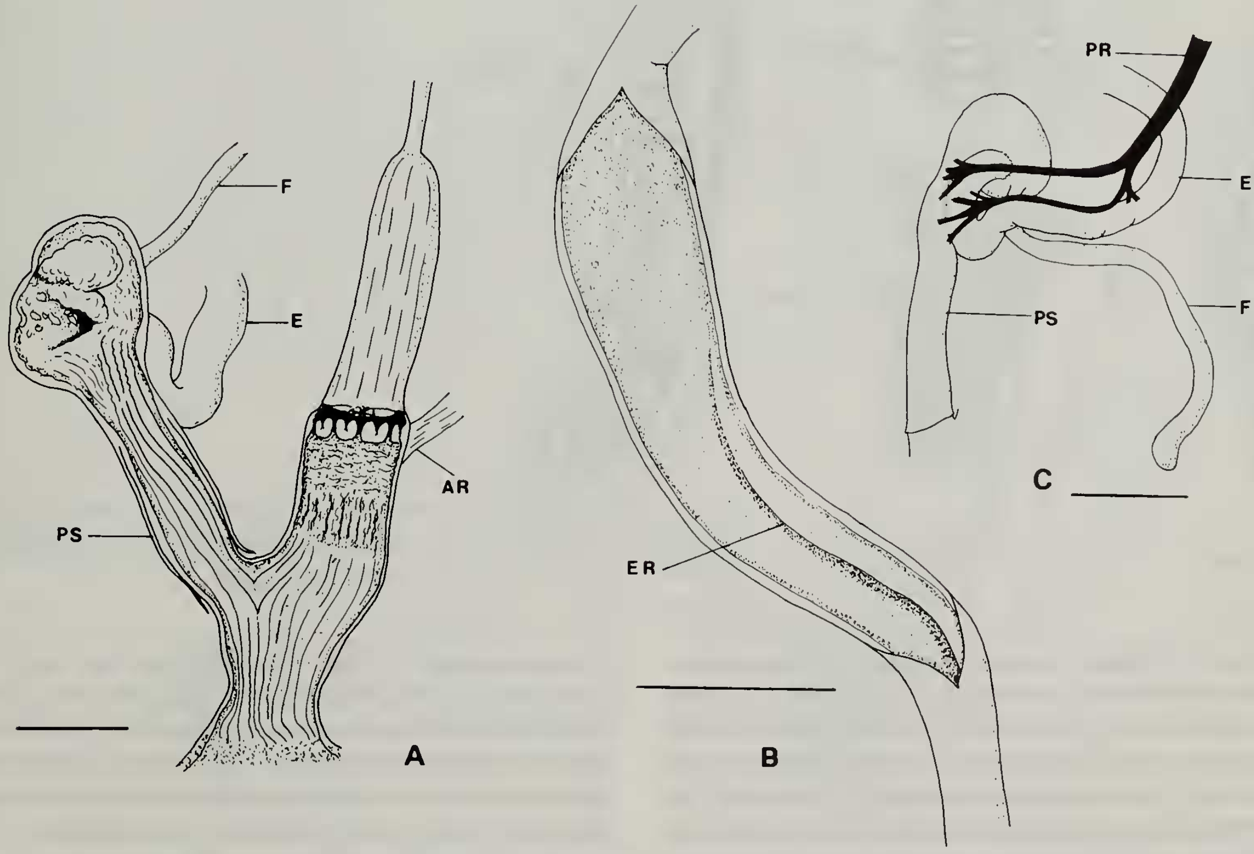

Fig. 17 A. Penis and appendix; B. Epiphallus; C. Penial retractor muscle. *Amimopina macleayi*, Daly River, Australia. Scale line 1 mm.

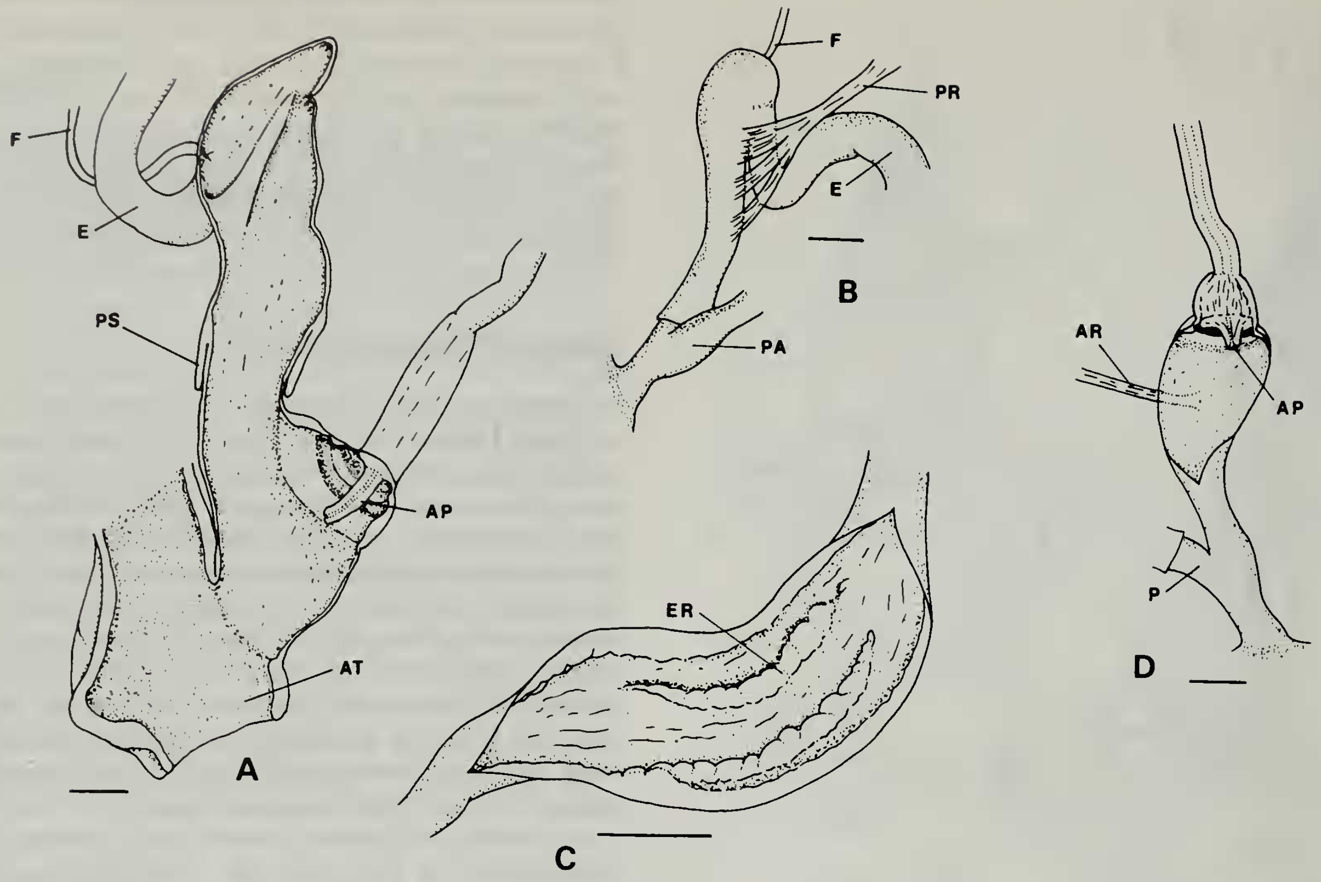

Fig. 18 A. Penis and appendix; *Rhachistia chiradzuluensis*, Thika, Kenya. B. Penis; C. Epiphallus; D. Penial appendix; *Rhachistia histrio*, Maré, Loyalty Islands. Scale lines 0.5 mm.

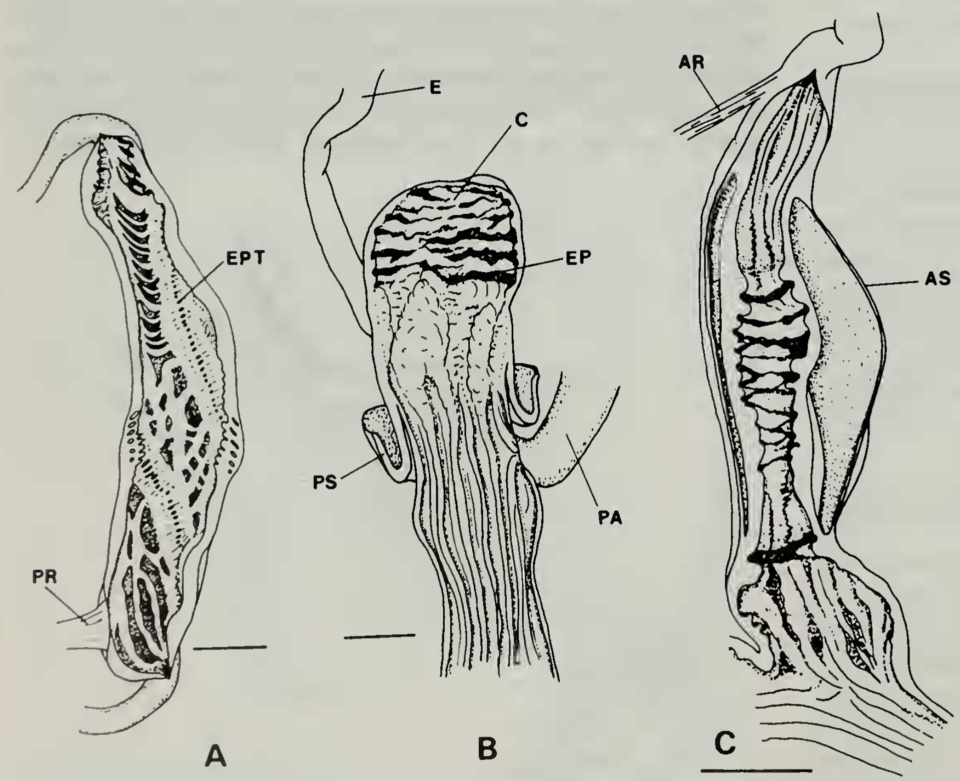

Fig. 19 A. Epiphallus; B. Penis; C. Penial appendix. *Cerastus trapezoidea*, Kitale, Kenya. Scale lines 1 mm.

progressively more divided towards margin. Three genera, *Pachnodus, Rhachistia* and *Amimopina*, have broad, blunt mesocones on the central and lateral teeth rather than the more-usual pointed cusps (Character 21), and a distinction is also made between the presence or absence of ectocones on the central tooth (Character 22), the former being the more-usual state. Other radular features, such as the development of raised, sharpened lateral ectocones, appear to be functional correlates of other modifications and so are not treated separately for the cladistic analysis. The prominently developed endocones in *Amimopina* (Solem, 1973) and the various types of modification which have taken place in the marginal teeth of certain genera, would appear as autapomorphies and therefore have been excluded from the analysis; they are, however, considered further in the discussion.

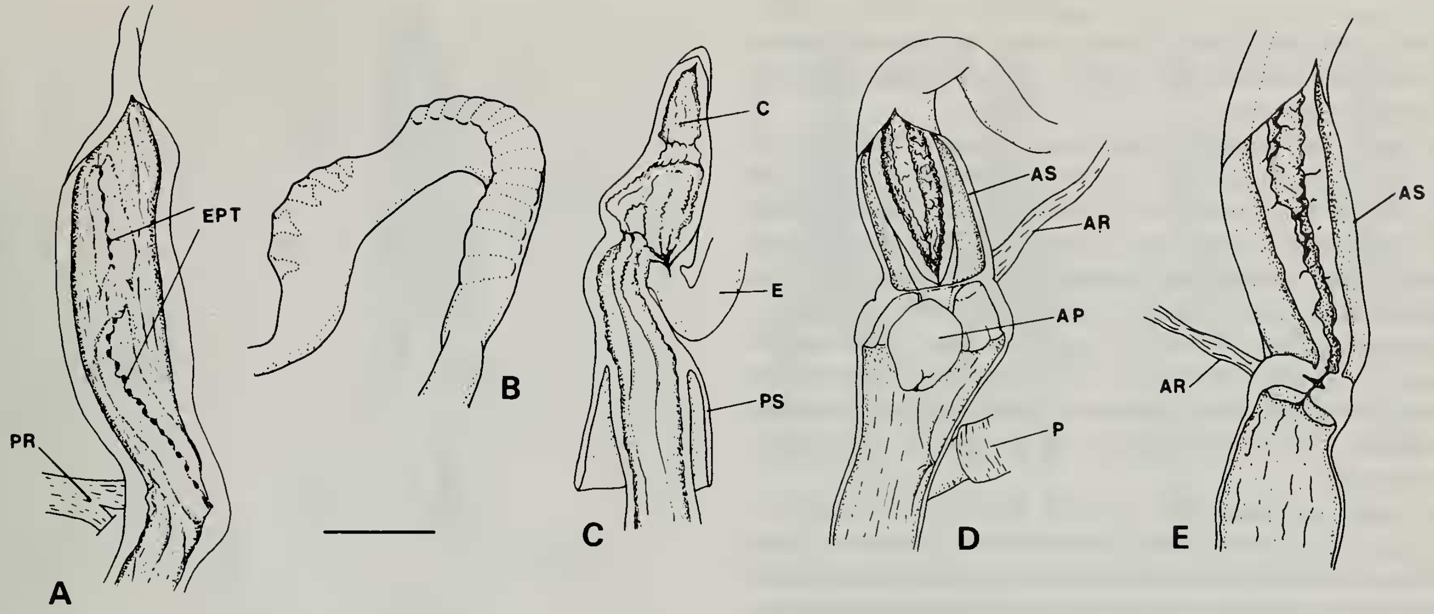

Fig. 20 A, B. Epiphallus; C. Penis; E. Penial appendix. *Conulinus rutshuruensis*, Thika, Kenya. D. Penial appendix. *Conulinus daubenbergeri*, between Marango and Kilimanjaro, Tanzania. Scale line 1 mm.

CLADISTIC ANALYSIS

Table 3 shows the matrix of the twelve taxonomic groups and twenty-two characters used for the cladistic analysis. The taxa represented are all generic units, with the exception of *Edouardia* where small and large species groups have been distinguished following Connolly (1939). Autapomorphic characters have been excluded as recommended by Swofford (1985). Most characters are scored as binary, but five (Characters 1, 2, 9, 10, 20) are represented as ternary. Of these latter characters, only Character 1 has been ordered (see above), the remainder being treated as unordered for the purposes of analysis. No attempt was made to weight the characters. The analysis was undertaken using the PAUP program of Swofford (1985), Version 2.4.1, which is based on the Wagner criterion that the best tree is the shortest or most parsimonious (*ie.* that involving the fewest number of character-state changes or steps). The matrix size was sufficiently small for the branch-and-bound algorithm (based on Hendy & Penny, 1982) to be used. This algorithm purports to obtain all the most parsimonious trees (Swofford, 1985) although Platnick (1987) has shown that this is not always the

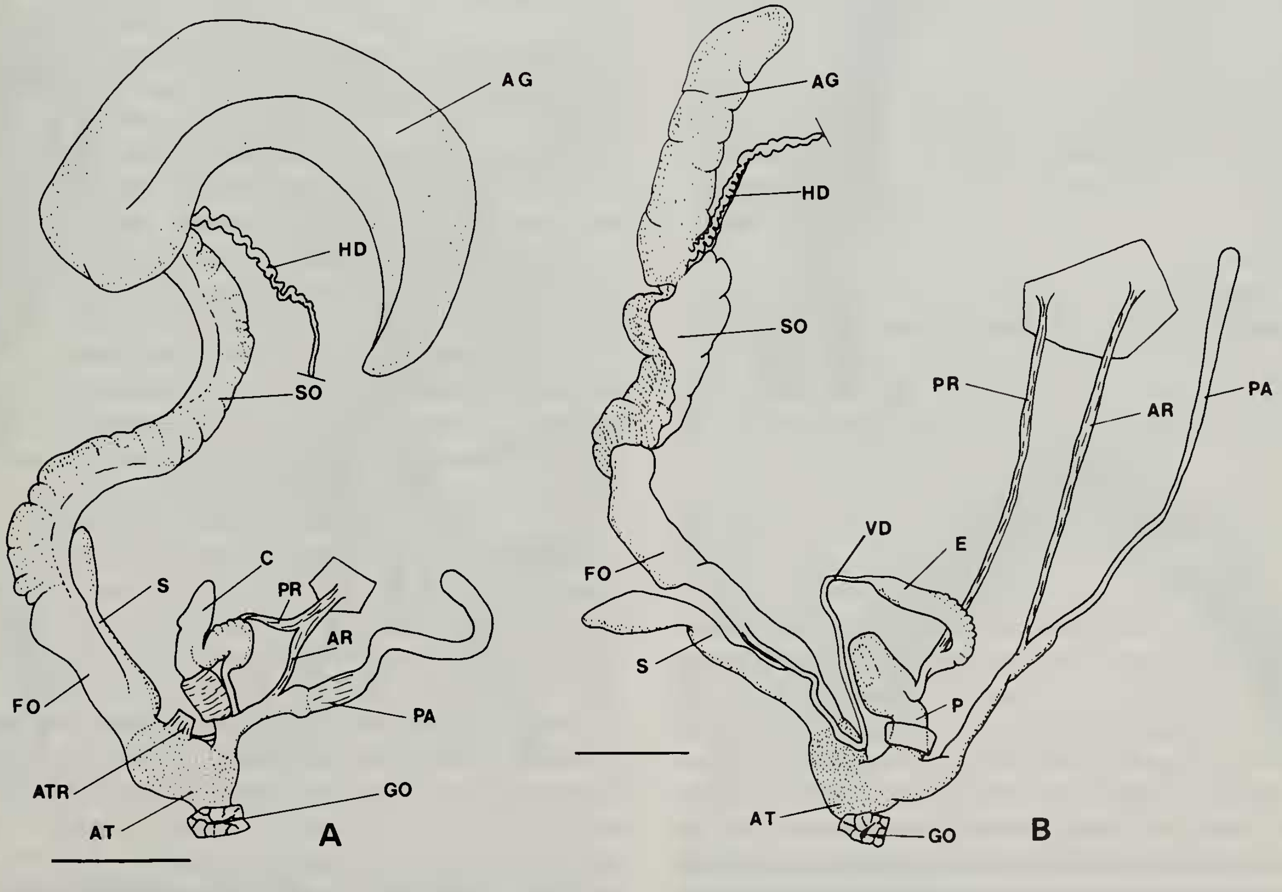

Fig. 21 Genital systems. A. *Rachis punctata*, Dar es Salaam, Tanzania. B. *Achatinelloides sosotrensis*, Socotra. Scale line 2 mm.

case. Following Platnick, all the available optimising options available under PAUP were used, as well as various levels of hold, and the BLRANGE option, but no additional trees were found in this way.

The PAUP run produced three equally parsimonious trees, each with a length of 42 steps and a consistency index of 0.643. Two of these trees are accounted for by an unresolved trichotomy involving the two groups of *Edouardia* with the *Rhachistia* and *Amimopina* pairing; in the third tree this trichotomy was resolved with the two *Edouardia* emerging as sister groups. This problem is perhaps best overcome by treating *Edouardia* as a resolved monophyletic taxon for the purposes of the following discussion, in which the character-state changes involved in this area of the tree are considered in more detail.

The resulting cladogram is shown in Fig. 28. The entire Cerastinae are separated from the designated outgroup (*Ena*) on the basis of six characters of the soft anatomy, three of which may be considered strong synapomorphies defining the subfamily: the presence of renal and rectal folds or ridges (Characters 1, 2) and of a pigmented atrial region (Character 13) are, with very few exceptions, characteristic of the whole group. There are also changes in epiphallar ornamentation (Character 4), with the development of a longitudinal row of spines, and in the insertion of the penial retractor which moves from the penis to the epiphallus (Character 9).

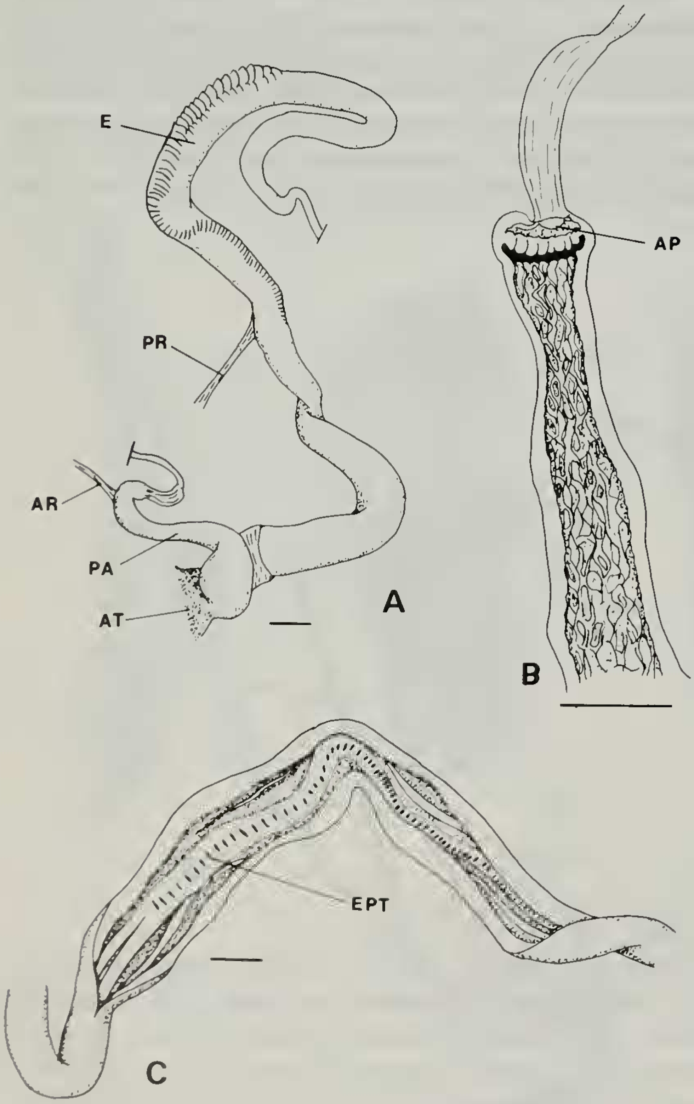

Fig. 22 A. Male terminal genitalia; B. Penial appendix; C. Epiphallus. *Pachnodus silhouettanus*, Shilouette, Seychelles. Scale lines 1 mm.

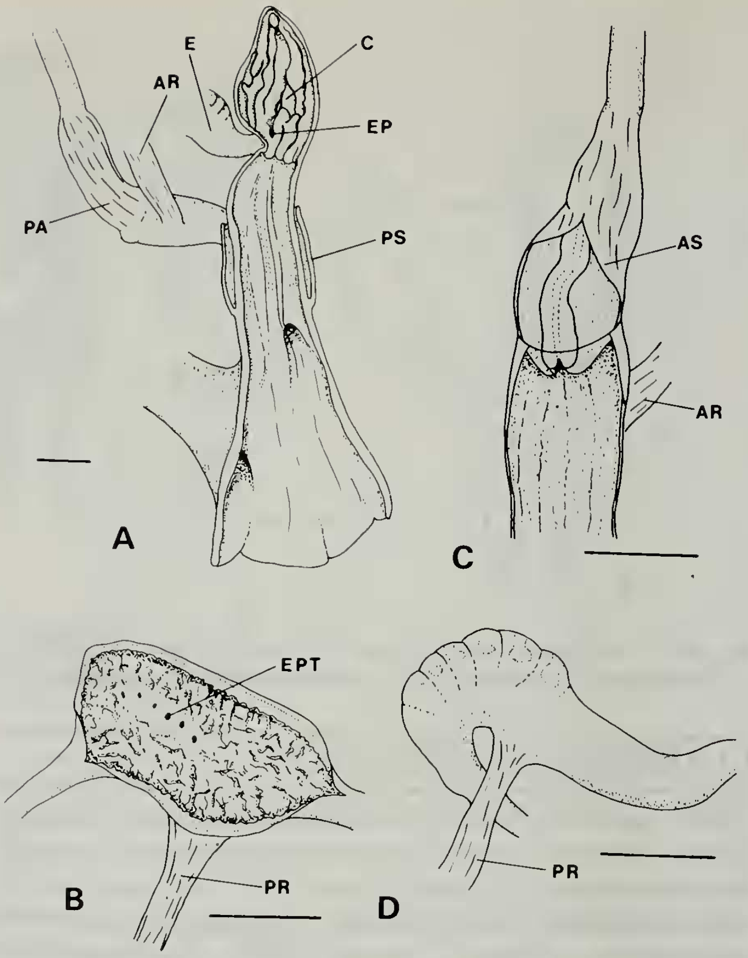

Fig. 23 A. Penis; B. Epiphallus, C. Penial appendix; D. Epiphallus. *Rachis punctata*, Dar es Salaam. Scale lines 0.5 mm.

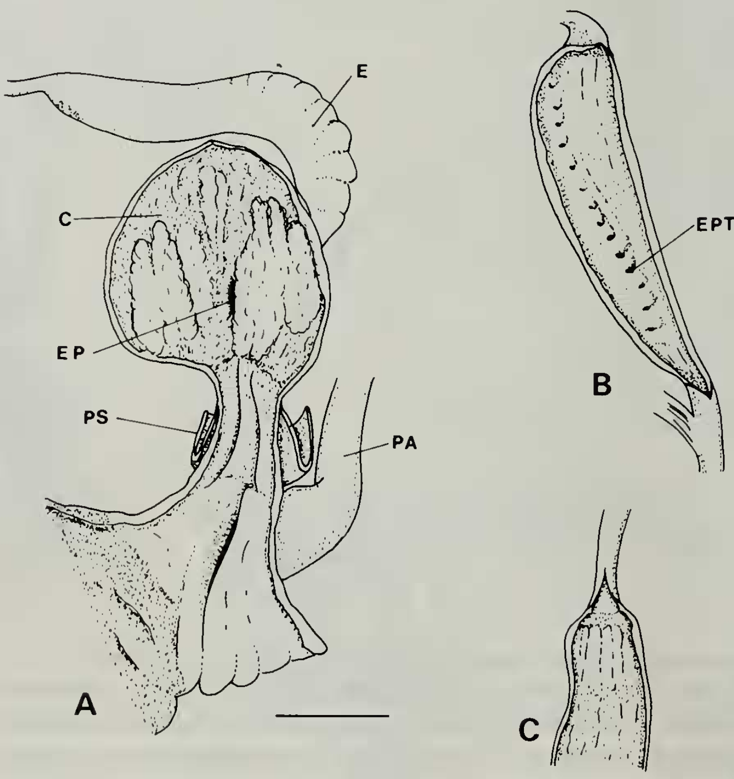

Fig. 24 A. Penis; B. Epiphallus; C. Penial appendix. *Achatinelloides balfouri*, Socotra. Scale line 1 mm.

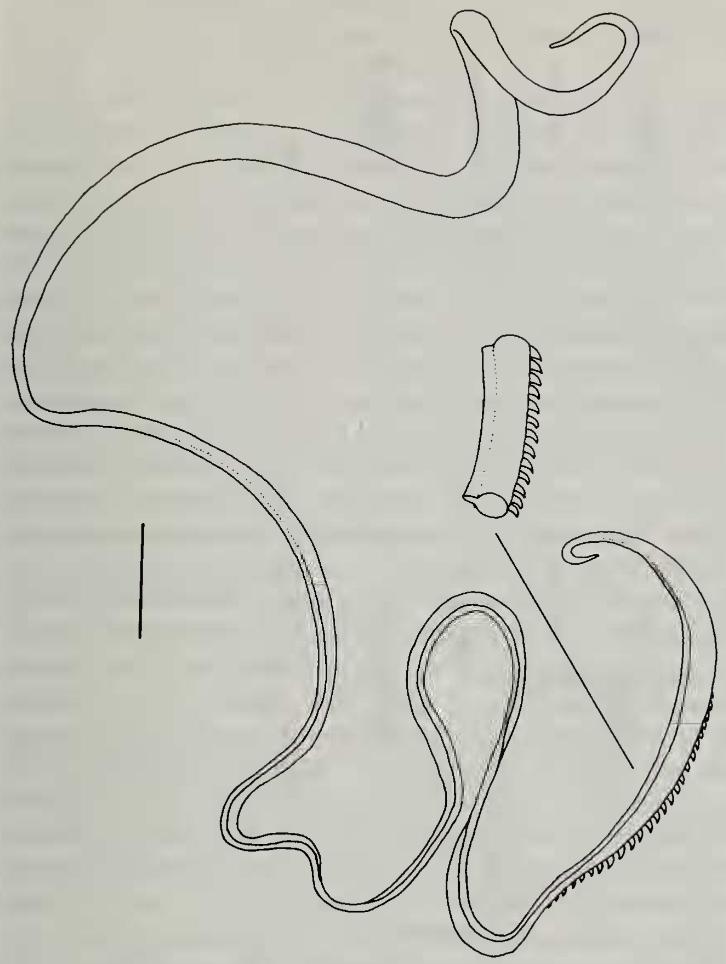

Fig. 25 Spermatophore. *Rhachistia rhodotaenia*, Nairobi-Mombassa Road, Kenya. Scale line 1 mm (for enlargement, 0.5 mm).

Additionally, an open umbilicus to the shell develops at this level of the cladogram (Character 19), which characterises of all but two of the genera.

The most primitive genus in the cladogram is *Pachnodus*, which lacks a penial caecum (Character 10). It does, however, possess a highly modified 'arboreal' radula (Characters 20–22) and a prominent tail crest (Character 14) which it shares with the two succeeding genera *Cerastus* and *Conulinus*. These two genera differ from *Pachnodus* in having a well-developed penial caecum (Character 10) which occurs in one of two basic forms throughout the remainder of the Cerastinae, and in modifications to the penial appendix (Character 6). *Conulinus* lacks the shell lip (Character 17) found in both *Pachnodus* and *Cerastus*. These three genera together form a relatively closely related group of primitive taxa, which can be contrasted with the more-advanced taxa which make up the rest of the cladogram. These remaining genera are separated into two quite distinct clades.

The first of these clades includes *Rachis, Zebrinops, Euryptyxis* and *Achatinelloides* and appears the more primitive, or at least the less differentiated of the two. It shares many features with the preceding genera *Cerastus* and *Conulinus*, notably in the terminal genitalia, but is separated in the tree on the basis of shell pigmentation (Characters 15, 16) and the base of the appendicular stalk which becomes unthickened (Character 5). *Rachis* retains joined penial and appendicular retractor muscles (Character 8) but in the three remaining genera these originate separately on the lower lung wall. *Zebrinops* is distinguished by having its retractor muscle inserted on the central stalk of the penial appendix (Character 7) rather than on its base, whilst *Euryptyxis* and *Achatinelloides* form a terminal sistergroup united on the basis of a secondarily unenclosed base to the appendicular stalk (Character 6) and, uniquely in the cladogram, a well-developed columellar fold and completely closed umbilicus on the shell (Characters 18, 19). *Euryptyxis* shows two reversals in shell characters, losing colour patterning (Character 16) and developing an often very pronounced apertural lip (Character 17).

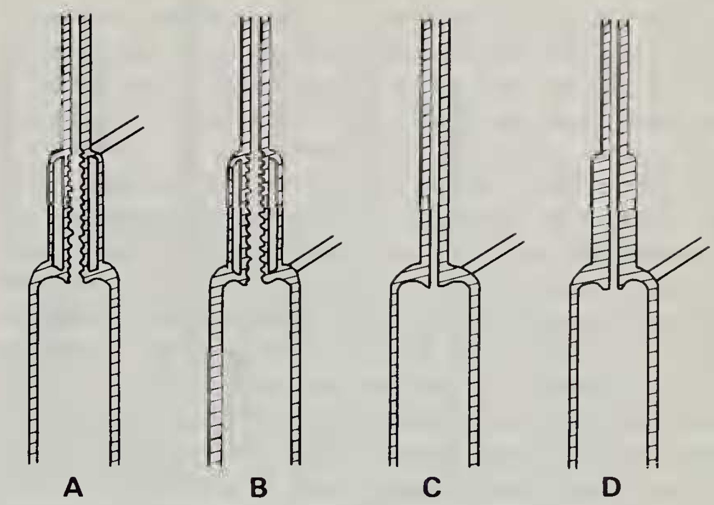

Fig. 26 Diagramatic representation of structural patterns at the junction of the basal and central portions of the cerastine penial appendix.

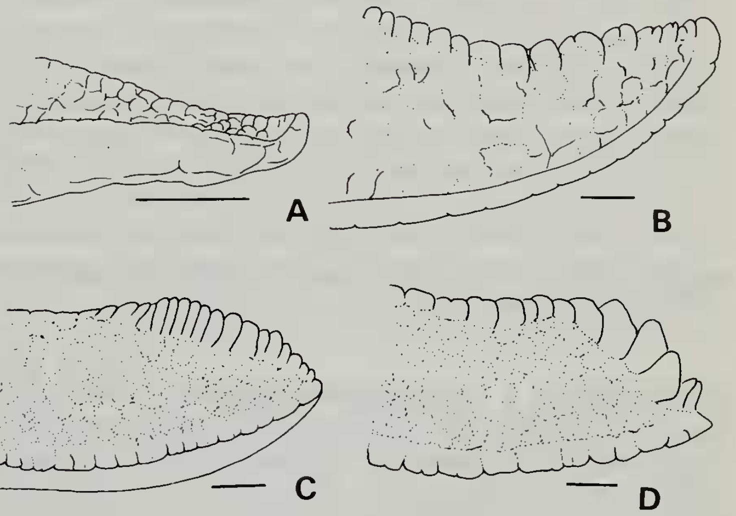

Fig. 27 Tail and tail crest. A. *Edouardia tumida*, Mombassa Island, Kenya; B. *Conulinus rutshuruensis*, Karura Forest, Nairobi, Kenya; C. *Pachnodus silhouettanus*, Silhouette, Seychelles; D. *Cerastus somaliensis*, Daloh Gudun, Somali Republic. Scale line 1 mm.

The second clade comprises the three genera *Edouardia, Amimopina* and *Rhachistia*. These form a strongly differentiated group of closely related taxa, separated in the cladogram by no less than eight character-state changes. Of these, seven can be considered to characterise the clade as a whole. The renal fold fuses to the kidney wall along most of its length to form a ureteric tube (Character 1), the so called 'pseudosigmurethrous' condition (Solem, 1964). All three genera have a reduced spermathecal stalk (Character 3) and secondarily simplified epiphaller ornamentation of longitudinal ridges rather than pits (Character 4), as well as a modified penial

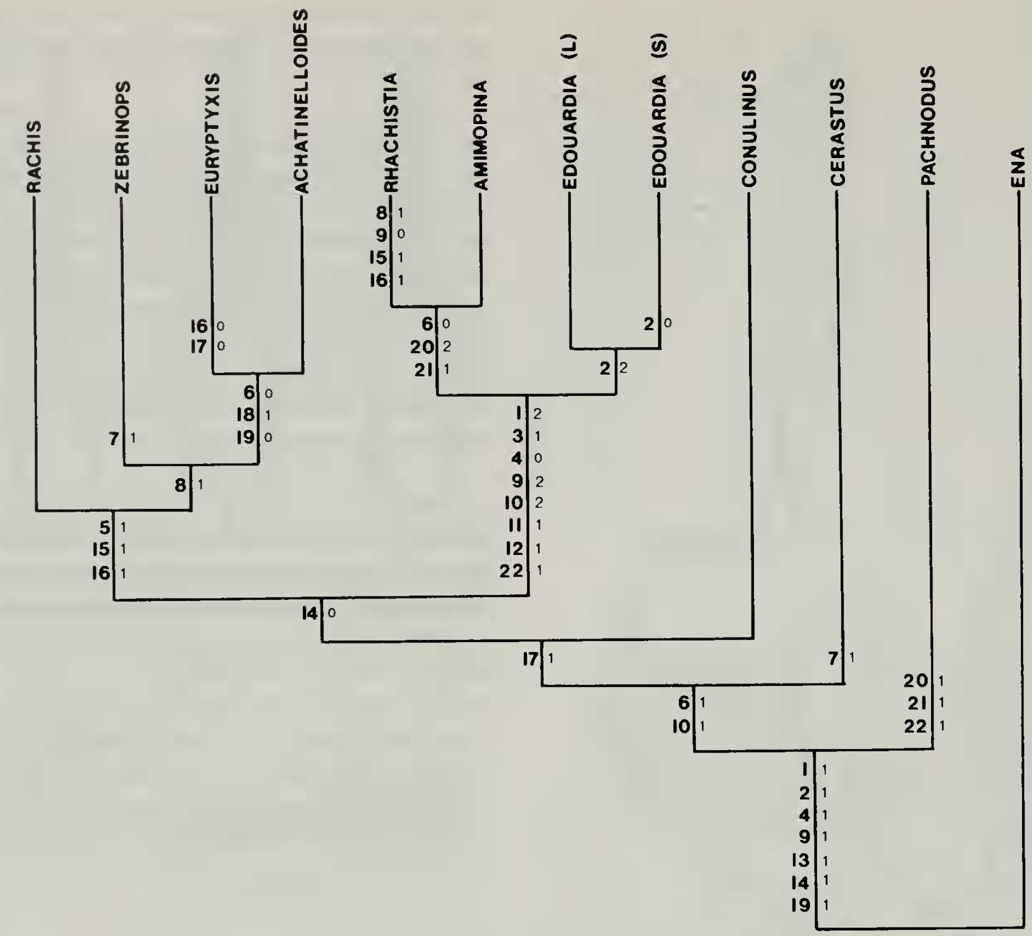

Fig. 28 Cladogram of cerastine genera. Characters are numbered at each node from 1–22 in bold, character states from 0–2 in feint.

caecum bearing a well-developed flagellum (Characters 10, 11, 12). In addition, the ectocones on the central tooth of the radula are lost (Character 22). The small and large groupings of *Edouardia* form part of an unresolved trichotomy in two of the trees, but are resolved in the third where they are paired as a sister group; the former show complete loss of the rectal fold (Character 2), as do many *Rhachistia*, whilst in the large forms the fold is only partially reduced to a thin ridge. Both share with *Amimopina* a double insertion of the penial retractor muscle onto the penis and epiphallus (Character 9) which is subsequently reversed in *Rhachistia*. *Amimopina* retains the complete rectal fold (the plesiomorphic cerastine condition of Character 2), but is united as a sister group with *Rhachistia* in all three trees as both share a simplified base to the appendicular stalk (Character 6) and similar modificiations to the shape of the radular rows, as well as of the individual teeth (Characters 20, 21). *Rhachistia* differs from *Amimopina* in having a pale, patterned shell (Characters 15–16), and also in having a separate origination of the penial and appendicular retractor muscles (Character 8) and a single insertion of this muscle onto the penis (Character 9).

DISCUSSION

The results of the cladistic analysis lend strong support to the hypothesis that the Cerastinae represent a monophyletic taxon in the sense of Hennig (1966), their monophyly being firmly based on a series of independent anatomical characters of the reproductive and excretory systems. Moreover, the cerastines differ from the northern Enidae (the selected outgroup) in a number of additional features, such as the presence of a muscular penial sheath and the absence of a mantle gland and hermaphrodite-duct diverticulae, which did not show variation between genera and therefore were not used in the analysis, but which nevertheless represent taxonomically informative characters. A consideration of the wider significance of reproductive, excretory and shell features in the evolution of the Orthurethra has been given by Nordsieck (1985; 1986).

Two broad groups of taxa can be distinguished in the cladogram: a main lineage of genera possessing open renal and rectal grooves in the pallial cavity, and a second, well-defined clade which branches off above the three basal genera in the cladogram. This second group comprises three genera, *Edouardia*, *Rhachistia* and *Amimopina*, all of which have a closed, pseudosigmurethous ureteric tube. These various changes to the cerastine excretory system have given rise to a more-complex pallial arrangement than is found in any other orthurethran group, and which perhaps represents the most characteristic feature of the Cerastinae as a whole. Although a few other orthurethran genera such as *Acanthinula* have developed a closed renal ureter (Watson, 1920), the complete rectal fold or ridge of the cerastines which runs the full length of the lung, apparently is unique within the Orthurethra. In life these pallial folds would delimit excretory from respiratory areas within the cavity, and thus presumably increase the efficiency of both systems. The partial or complete closure of the renal fold would appear to be a further adaptation to xerophilic conditions. It is associated with a tendency towards reduction or even complete loss of the rectal fold in some species of *Edouardia* and *Rhachistia*, but the reasons for this are unclear.

The precise adaptive functions of many of the critical reproductive features are similarly obscure. In the female system, the extreme reduction of the spermathecal stalk found in the pseudosigmurethrous group, and the development of the highly characteristic pigmented spongy tissue in the atrium/vagina of all genera are both of uncertain significance, although the latter becomes everted at copulation and may well have a secretory function. The spermatheca is used to store and then break down the spermatophore after copulation, and in many northern enids exceptionally long spermatophores are housed in a special spermathecal diverticulum branching off the main spermathecal stalk. It is therefore surprising that spermathecal stalk reduction in the pseudosigmurethrous cerastines should be associated with the relatively long spermatophores found in this group, and that a spermathecal diverticulum is not known in the Cerastinae.

Some of the most intriguing changes in the reproductive system have taken place in the terminal male genitalia. A muscular penial sheath was found in all dissected cerastine genera, but does not appear to have been recorded in any other orthurethran group. It is presumably associated with evertion of the penis and possibly also ejection of the spermatophore, but its development varies enormously between genera. This sheath (not to be confused with the 'penial sheath' of Nordsieck (1985) which is simply the lower part of the penial tube, or the sheath which encloses the base of the penial appendix in certain cerastine genera) is wanting in northern enids and thus probably represnts a synapomorphy of the Cerastinae.

The only structure in other Orthurethra which in any way resembles the cerastine penial flagellum (which characterises all the pseudosigmurethrous taxa) is the 'flagellum' of *Solatopupa* and *Granaria* (Steenberg, 1925; Gittenberger, 1973), or perhaps the paired weak 'diverticula' in *Acanthinula* (Steenberg, 1917). However, in neither case do these approach the extreme size of the flagellum found in *Edouardia* or *Rhachistia*. Gittenberger (in. litt.) states that the chondrinine flagellum appears to result from the growing together of the penial and epiphallian tube at the point where the loop of the male part of the genitalia typically curves, and considers that this condition is not homologous with that of the Cerastinae. This latter is also reminiscent of the short appendix found in the New Caledonian charopid *Pararhytida*, which was hypothesised to have a secretory function (Mordan & Tillier, 1986). The cerastine flagellum is a fairly simple structure which, unlike the penial appendix, does not appear to be eversible, and this type of organ seems to have been developed independently in a number of stylommatophoran lineages. On the evidence of the reproductive anatomy figured by Zilch (1972; Fig. 5), the west African genus *Altenaia* should be included in the pseudosigmurethrous group as it too has a flagellate penis. *Altenaia* also lacks a pronounced spermathecal stalk, a further characteristic of this clade.

A highly distinctive and elaborate penial appendix is developed in numerous orthurethran groups, and the close structural similarities suggest that this organ, unlike the flagellum, is homologous throughout the suborder. In the Cerastinae it has undergone considerable change in its lower region involving elaboration of the wall of the lumen at the base of the central stalk, as well as enclosure of this area of the stalk by a muscular sheath. These changes are found in *Cerastus* and *Conulinus*, and apparently are retained as a primitive character in *Edouardia* on the one hand, and *Zebrinops* and *Rachis* on the other. The appendicular retractor muscle has also moved upwards onto the top of the sheath in *Cerastus* and, less obviously so, in *Zebrinops*, but this appears to have taken place independently in the two genera. This arrangement would suggest that the tip of the central stalk as well as the basal portion of the appendix protrudes when the appendix is everted; such an interpretation would not only explain the presence of a muscular sheath, but also the internal sculpturing which would serve to increase the surface area of the everted tip. It is noticeable also that the elaboration of the stalk base in *Cerastus* is associated with a very short basal region to the appendix. These changes could perhaps be most readily understood if the appendix had taken over the intromitent function of the penis as it has in, for example, *Sagda* (Goodfriend, 1986), but this does not appear to be the case in the Cerastinae. Block (1968) has observed copulation in *Zebrinops*, where the penial appendix is everted, but not inserted into the partner; rather, it extends under the shell to the region of the mantle collar. Block suggested that it might function as a stimulator and also act to locate the genital orifice. Mordan (pers. obs.) witnessed copulation in the closely related genus *Euryptyxis*, and observed a similar behaviour pattern. In one individual of the mating pair the everted appendix was inserted under the partner's shell, but in the other the tip of the appendix was applied to the skin just behind the genital orifice of the partner, onto which it secreted a milky white fluid. This fluid did not contain sperm, but it is possible that it included some stimulatory secretion similar to that recorded by Chung (1986) from the mucous glands of *Helix*.

From the analysis it would appear that a joined origin of the penial and appendicular retractor muscles represents the plesiomorphic condition within the Cerastinae, only becoming separated in some of the more-advanced genera. This separation has arisen independently on at least two occasions. Some support for the primitiveness of joined retractors in the Orthurethra is given by an ontogenetic study of *Achatinella* in which the retractors start as a single muscle and become progressively more separated as the animal matures (Pilsbry, Cooke & Neal, 1928).

Shell characters were also utilised in the analysis but, not unexpectedly, showed a high level of homoplasy. In general there was a trend towards paler and more-patterned shell colouration in advanced genera of both terminal clades, associated with an arboreal or more-open habitat preference. This relationship between shell pigmentation and habitat has been well documented in other land-snail groups (*eg*. Woodruff, 1978, for *Cerion*). *Euryptyxis* and *Achatinelloides* were united as sister-taxa largely on the basis of two, shared shell characters: a wide but closed umbilicus and a prominent visible columellar fold. These features are also shared with *Passamaella*, a cerastine genus whose anatomy is now known but which, like *Achatinelloides*, is a Socotran endemic, and it is reasonable to assume that these groups are closely related.

One of the main conclusions to be drawn from the cladistic analysis was the closeness of relationship shown between the genera in the pseudosigmurethrous clade, particularly when compared with their high degree of differentiation from other cerastines. Large carinate *Edouardia* from southern Africa were united with the more-widespread, smaller *Edouardia* either as part of an unresolved trichotomy, or as sister groups in the third tree. This last tree was resolved by assuming that the two *Edouardia* groups shared a reduced rectal fold, which is subsequently lost in the smaller species. Such secondary reduction and then loss of the fold is not an unreasonable hypothesis, although the adaptive value of such a change is not obvious.

The genus *Rhachistia* was introduced by Connolly (1925: 163) to include a number of species previously placed in *Rhachidina. Rhachistia* was separated by Connolly on shell and radular characters, and in particular by having a radula 'of a specialised arboreal type'. In general the radulae of cerastines are remarkably uniform in appearance, and similar to those of the northern Enidae (Mordan, 1986, fig. 5), but the type species of *Rhachistia, R. rhodotaenia*, does have unusually sharply angled tooth rows and broad, blunt cusps on the centrals and laterals. In this respect it differs markedly from the type species of *Rhachidina, R. tumefacta*, as figured by Thiele (1921; p. 1.4, fig. 2). Of the fourteen species whose radulae were examined and which have been attributed to one or other of these two genera, only *usagarica* Smith from East Africa appears certainly to belong to *Rhachidina*. All the rest have a radula of the *Rhachistia* type. Thiele's figure of *tumefacta* shows that it develops prominent endocones on the lateral teeth, as does *usagarica*, a feature shared only with *Amimopina*. Both *usagarica* and *tumefacta* also have a clearly developed apertural lip on the shell, and this is probably characteristic of the genus. None of the non-African species in the *Rhachistia/Rhachidina* complex have this lip, and thus it would seem that *Rhachidina* is a very much more restricted genus than previously believed, perhaps comprising only a small number of exclusively African taxa. However, its precise limits and relationships cannot be resolved until details of the soft anatomy of *tumifacta* are known.

Amimopina is represented as the sistergroup of *Rhachistia*, the relationship being based in part on shared possession of a modified radula of the arboreal type. Although this is represented in the cladogram as a synapomorphy for the group, Solem (1973) has argued from a detailed analysis of scanning electron micrographs that the modifications have originated separately in these two groups, the main differences being in the inter-row support mechanism and the degree of ectoconal development in the lateral teeth. Whilst Solem's contention that the soft anatomy of the two is not similar, and therefore that they are only distantly related within the Enidae, is no longer tenable, it may nevertheless remain that certain radular modifications have been independently derived in the two genera. The 'arboreal' radula of *Pachnodus* clearly has evolved independently, for although it shows certain parallel similarities with that of *Rhachistia*, such as the blunt mesocones and sharp, raised ectocones on the lateral teeth, there are marked differences in row shape and in the form and number of the marginal teeth (van Mol & Coppois, 1980). In particular, the row of marginal teeth of *Pachnodus* is *backwardly* directed, whereas in *Amimopina* and *Rhachistia* the entire lateral and marginal rows are angled *forward* from the central tooth.

The three most primitive genera in the cladogram are *Pachnodus, Conulinus* and *Cerastus*; all are essentially forest/montane taxa, and this would therefore appear to be the most-likely ancestral habit of the Cerastinae. Judged by the present-day habitat preferences of the remaining genera, subsequent evolution should be viewed as a progressive trend towards a xerophilic life style. One feature which may be significant in this context is the caudal crest, which is only present (or at least only prominently developed) in *Pachnodus, Cerastus* and *Conulinus*. Its function is unknown, but it resembles the paired tail crests of some subulinids (Odhner, 1921) and, to a lesser degree, the 'keel' of limacid and milacid slugs. No equivalent structure appears to have been recorded from other Orthurethra. It would seem to represent a primitive feature of the Cerastinae which has been subject to selection for reduction and ultimately loss in the more xerophilic genera, possibly because one of its effects would be to increase the evaporative surface-area of the tail.

Although the general pattern of relationships in the cladogram appears to be fairly robust (for example, the plesiomorphy of *Pachnodus*; the subsequent division into distinct pseudosigmurethrous and non-pseudosigmurethrous clades; and the terminal sister-group relationship of Socotran endemics with Arabian genera), the impression given in other parts of the cladogram is of mosaic evolution and, as a result, a topology which appears rather unstable in that it is based on a small number of often weak characters. This is particularly true of relationships within the pseudosigmurethrous clade, even though the monophyly of this particular clade has been very clearly established.

ACKNOWLEDGEMENTS. I would like to thank Edmund Gittenberger, Alan Solem and Simon Tillier for their valuable comments on earlier drafts of this paper. I am also grateful to Dai Herbert and Richard Kilburn of the Natal Museum, Pietermaritzburg, for the provision of material.

APPENDIX 1

List of material dissected

Achatinelloides balfouri. Socotra. Leg. Prof B. Balfour. 2 spec.

Achatinelloides socotrensis (L. Pfeiffer). Bed of River Hanifa, 2 miles Hadibo, Socotra. Leg. Oxford University Socotra Expedition, 11.viii.1956. 3 specs. Reg. No. 1957.7.10.1–3. 3 specs.

Amimopina macleayi (Brazier). Cameron's Bay, Darwin, Northern Territory, Australia. Leg. V. Kessner, 1.xi.1981. 2 immature specs.

Amimopina macleayi. Oolloo Crossing, E. bank of Daly River. Northern Territory, Australia. Leg. V. Kessner, 16.iii.1986. FMNH 215272/17. 2 specs.

Amimopina macleayi. N.W. tip Putairta Hill, Kimberley, Western Australia. Leg. A. Solem, L. Price, W. Emberton, 8.vi.1984. FMNH 211955/2. 2 immature specs.

Cerastus trapezoidea (Martens). Kitale, Kenya. Leg. Mrs R. Tweedie. 1 spec.

Cerastus somaliensis (E.A. Smith). Daloh Gudun, Somali Republic. Leg. C.F. Hemming. 2 specs.

Conulinus daubenbergeri (L. Pfeiffer). Rain Forest between Marango and Kilimanjaro, Tanzania, 2200m. Leg. and det. K.L. Pfeiffer. 1 spec.

Conulinus rutshuruensis (Pilsbry). Karura Forest, Nairobi, Kenya. Leg. Polhill, 20.v.1960. 1 spec.

Edouardia sordidula (von Martens). Wazo Hill, nr Dar es Salaam, Tanzania. Leg. P.F. Kasigwa. 1 spec.

Edouardia tumida Taylor. Mombassa Island, Kenya. Leg. B. Verdcourt, ix.1962. 3 specs.

Edouardia natalensis (Pfeiffer). Pietermaritzburg, South Africa. 3 specs.

Edouardia cf. *metula* (von Martens). Bally, Nairobi, Kenya. Leg. B.

Verdcourt. 2 specs.

Pachnodus silhouettanus (van Mol & Coppois). Silhouette, Seychelles. Leg. E.S. Brown, 15.ii.1953. 1 spec.

Rachis punctata (Anton). Dar es Salaam, Tanzania. Leg. W.E. Calton, xi.1956. 3 specs.

Rachis punctata. Sabaki, Nr Malindi, Kenya. Leg. R. Polhill, xi. 1961. 1 spec.

Rhachistia histrio Pfeiffer. Maré, Loyalty Islands. Leg. W.W. Perry. Reg. No. 1875.11.3.1. 2 specs.

Rhachistia chiradzuluensis (E.A. Smith). Chania Gorge, Thika, Kenya. Leg. B. Verdcourt, det B. Verdcourt. 1 spec.

Rhachistia chiradzuluensis. Thika, Kenya. Leg. B. Verdcourt, v. 1960.

Rhachistia aldabrae (von Martens). Aldabra Atoll. Leg. G.Lionnett, det B. Verdcourt.

Rhachistia rhodotaenia (von Martens). Nairobi-Mombassa Road, Kenya. Leg. R. Polhill and B. Verdcourt, 17.iv.1960. 3 specs.

Zebrinops maunoiriana Bourguignat. Erigavo, Somali Republic. Leg. C.F. Hemming. 2 specs.

Zebrinops maunoiriana. 1 mile SE of Shiek, Somali Republic. Leg. C.F. Hemming. 1 spec.

APPENDIX 2

Abbreviations used in figures

A	Anus	HG	Hermaphrodite gland
AG	Albumen gland	K	Kidney
AP	Appendicular papilla/pore	MC	Mantle collar
AR	Appendicular retractor muscle	P	Penis
		PA	Penial appendix
AS	Appendicular sheath	PN	Pneumostome
AT	Atrium	PR	Penial retractor muscle
AU	Auricle	PS	Penial sheath
C	Caecum	RNF	Renal fold
E	Epiphallus	RNU	Renal ureter
EPT	Epiphallar pit	RT	Rectum
ER	Epiphallar ridge	RTF	Rectal fold
F	Flagellum	S	Spermatheca
FO	Free oviduct	SO	Spermoviduct
GO	Genital orifice	PV	Pulmonary vein
HD	Hermaphrodite duct	VE	Ventricle

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